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Saving for a Rainy Day: Influence of Environmental and Social Factors on Food Hoarding
Strategies in Free-Living Western Gray Squirrels (*Sciurus griseus*)

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Biology

by

Amanda Nicole Robin

2023

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ABSTRACT OF THE DISSERTATION

Saving for a Rainy Day: Influence of Environmental and Social Factors on Food Hoarding
Strategies in Free-Living Western Gray Squirrels (*Sciurus griseus*)

by

Amanda Nicole Robin

Doctor of Philosophy in Biology

University of California, Los Angeles, 2023

Professor Peter Nicholas Nonacs, Chair

Animals must deal with fluctuations in food availability across time. Long-term food hoarding species solve this problem by storing food in times of abundance. This turns a formally fleeting resource temporally concentrated at a singular time point, into a sustainable life source. Food-hoarding is a cognitively demanding task that requires individuals to account for competing variables to meet immediate and future needs. The first step in hoarding is the choice to eat or cache. This dissertation investigates the influence of environmental factors, individual experiences, and social competition on eat-cache decisions within a marked population of free-living western gray squirrels (*S. griseus*). Squirrels were presented with a feeding station that provided a choice between a cacheable in-shell item and a minced item only suitable for immediate consumption. Chapter 1 reviews recent studies on the socioeconomics and cognition

of food hoarding in tree squirrels. These studies collectively inform the theoretical framework upon which this research is built. Chapter 2 examines the impact of time at varying scales. The eat-cache decision involves the interplay of factors such as satiety, food quality, competition, and predation risk. Results demonstrate that overlaid onto these considerations are seasonal variations in food abundance and immediate energy needs, along with the number of items already handled, and the assessment of item storability. Chapter 3 explores the influence of the presence of other squirrels on eat-cache decisions. Findings indicate a reduction in caching behavior when potential observers are present, highlighting squirrels' sensitivity to competition and their adeptness at integrating this information into their decision-making processes. Overall, this dissertation contributes to our understanding of the decision-making processes in a food-storing species through the collection of thousands of individual decisions in a natural setting.

The dissertation of Amanda Nicole Robin is approved.

Daniel T. Blumstein

Noa Pinter-Wollman

Jennifer Smith

Peter Nicholas Nonacs, Committee Chair

University of California, Los Angeles

2023

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For Chapter 2, Amanda Nicole Robin and Cynthia L. Frausto collected the data. Amanda Nicole Robin conducted the data analysis and wrote the manuscript. Amanda Nicole Robin and Peter Nonacs edited the manuscript.

For Chapter 3, Amanda Nicole Robin collected the data, performed the data analysis, and wrote the manuscript. Amanda Nicole Robin and Peter Nonacs edited the manuscript.

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- Advised director on operational decisions of the network.
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Community College Field Biology Alliance | Founder & Director **2018-2023**

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- Manage volunteer team and relationships with community partners and other stakeholders to design and implement program.
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UCLA Life Sciences Excellences Award in Educational Innovation	2020
National Science Foundation Graduate Research Fellowship	2017

Publications

- Robin, A.N., Farmer, A., O'Connell K., Varty, A., Hewlett, J., Lee, J. (2022) Community College Students in the Field: A review of a Community Conversation on Successful Programs and Strategies. *Bulletin of the Ecological Society of America: 103(3)*.
- Robin, A. N. & Jacobs, L.F. (2022). The socioeconomics of food hoarding in wild squirrels. *Current Opinion in Behavioral Sciences, 45, 101139*.
- Robin, A. N., Denton, K. K., Horna Lowell, E. S., Dulay, T., Ebrahimi, S., Johnson, G. C., ... & Nonacs, P. (2021). Major Evolutionary Transitions and the Roles of Facilitation and Information in Ecosystem Transformations. *Frontiers in Ecology and Evolution, 866*.

Selected Research Talks

- Robin AN & Smith EJ. Uncovering hidden belowground behaviors: A field test of machine learning algorithms on accelerometer data. Animal Behavior Society 2021.
- Robin AN & Nonacs P. The presence of others may shape the economic decision making of a food-storing arboreal squirrel. Society for Integrative and Comparative Biology Virtual Conference. 2021
- Robin AN, Lessig E, & Frausto C. Increasing Diversity Through Community College Student Engagement: A Student-Run Organization Model. Animal Behavior Society 2020.

Invited Presentations

- | | |
|--|-------------|
| National Association of Geoscience Teachers | 2023 |
| <ul style="list-style-type: none">Exploring models for engaging community college students in field research: a discussion of benefits and challenges. | |
| Undergraduate Field Experience Research Network | 2021 |
| <ul style="list-style-type: none">Community Colleges in the Field: Successful Programs and Strategies | |
| Frontiers in Ecology and Evolution | 2021 |
| <ul style="list-style-type: none">Major evolutionary transitions and the roles of facilitation and information in ecosystem transformations | |

Chapter 1

The Socioeconomics of Food Hoarding in Wild Squirrels

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Abstract

A food-hoarding squirrel reshapes its physical environment through storing food. These changes have ramifications for future economic decisions that cascade into social and reproductive consequences. Food-hoarding strategies exist on a continuum from concentrated caches in a defended larder to scattered caches defended using memory and olfaction. These strategies emerge in response to specific physical environments. Because caches are pilfered, the hoarder must also respond to the competitive social environment. Here, we review recent studies, both from captivity and the field, on the socioeconomics and cognition of hoarding in tree squirrels and chipmunks. As ubiquitous inhabitants of an increasingly urbanized world, these studies illuminate the theoretical and applied research potential of the study of such decisions in squirrels.

Introduction

A food hoarder converts a seasonal surplus of food to a resource more evenly distributed across time. By altering its physical environment in this way, it also changes its own ecological niche and hence evolutionary trajectory as the new niche demands new adaptations of behavior and cognition (Steele & Yi, 2020). Because hoarding artificially concentrates a valuable resource, it also increases social competition by attracting intruders and pilferers. Hence food hoarding, even in an apparently solitary species, is a process that emerges from social selection (Jacobs, 2009). Because food hoarding instigates this cascade of evolutionary changes, cognition in food hoarders is shaped by interactions between the physical environment, foraging economics, and social competition.

Wild squirrels (Order Rodentia, Family Sciuridae) offer an excellent opportunity to study these phenomena. Squirrels have adapted to urban and non-native habitats (Peplinski & Brown, 2020) and demonstrate diversity and complexity in food- hoarding behaviors. This offers an opportunity to study how socioeconomic decisions adapt over short and longtime spans, not only in hoarding behaviors but also in studies of fear (Uchida et al., 2019), predator responses (Twining et al., 2020; Wauters et al., 2019), and problem solving (Chow, Clayton, et al., 2021; Chow et al., 2018; Chow, Uchida, et al., 2021).

Two strategies anchor the spectrum of hoarding: larder and scatter hoarding. Larder hoarding is the multiple deposition of food items to a single cache site, such as a defended nest. Scatter hoarding is the strategy where each cache is created by a single deposition only, although the single deposition may later be moved to another location. In addition, squirrels may use a mixed strategy, employing both larder and scatter hoarding (Vander Wall, 1990) (Figure 1.1). A squirrel's economic decisions are constrained both by the physical challenges of foraging for hoardable foods and the social challenges that ensue once the forager has collected and concentrated these valuable food items. And because a scatter-hoarded seed not retrieved may grow into a tree providing future food (Steele & Yi, 2020), a squirrel's socioeconomic decisions in turn feeds back upon its physical environment.

Here, we ask how these three forces — physical environment, social environment, and economic risk — interact to produce the central bank strategy of the larder hoarder, the information economy of the scatter hoarder and the flexible decision processes in species using a mixed strategy (Figure 1.2).

The physical environment

Which hoarding strategy is used depends first on the physical world: the distribution of hoardable food (often tree seeds) and the plant's abilities to protect these seeds. Trees increase the cost of predation via chemical defenses (e.g., tannins and resins) and physical defenses (e.g., shell thickness) (Lichti et al., 2017; Steele & Yi, 2020). Tree species may also mast, unpredictably producing large or small numbers of seeds in a given year, a strategy that reduces the seed predator population. If not retrieved in time, cached seeds can escape predation via germination, further constraining the hoarder's options. Finally, the physical environment includes the challenges of winter: chipmunks hoard to survive hibernation and to compete in the spring breeding season, non-hibernating tree squirrels hoard to survive winter and compete in the winter breeding season (Steele & Yi, 2020).

The physical properties of multiple seeds packaged into cones allow the North American red squirrel (*Tamiasciurus hudsonicus*) to efficiently utilize a larder- hoarding strategy (Smith, 1968). Wild red squirrels cut, hoard, and consume unripe cones. Their jaw morphology reflects this arms race between conifers and predator: where cones are heavily armored to survive forest fires, the chewing apparatus is more robust (Steele & Yi, 2020). Consuming the cone seeds from a perch, the squirrel creates a midden, a pile of cone scales. The cold, wet midden becomes an ideal microhabitat to preserve cones and it thus increases in value as cone debris accumulates (Figure 1.1). This multiyear hoard allows the squirrels to survive years when cones are not produced. Female red squirrels appear able to perceive an upcoming mast year and will increase their litter size in anticipation (Dantzer et al., 2020; McAdam et al., 2019). Because midden-stored cone seeds cannot germinate, red squirrels can economically defend territories of even masting trees (Vander Wall, 1990).

In contrast, the seeds of deciduous tree species such as oaks and hickories germinate within months of being cached. Hence, mast seeding in deciduous tree seeds are too unpredictable in space and time to be economically defended as a territory. Further, because a scatter-hoarded seed that is not retrieved will have been planted in an advantageous location for its germination and survival, squirrel scatter-hoarding behaviors coevolve in concert with tree reproductive strategies (Lichti et al., 2017; Steele & Yi, 2020).

Scatter hoarding is a demanding strategy for squirrels that store their winter food supply but cannot defend a larder; it is ‘the best of a bad job’. Scatter hoarding presents new cognitive challenges: hoarders must strategize to retrieve caches more efficiently than their competitors, relying on memory and search strategies. Thus, the physical environment demands an information economy, where resources are defended by cognitive abilities. Scatter hoarders respond to a specific physical environment by using a range of hoarding strategies. Large tree squirrels adapted to deciduous tree species are often obligate scatter hoarders, such as the North American eastern gray squirrel (*Sciurus carolinensis*) and fox squirrel (*S. niger*) and the Eurasian red squirrel (*S. vulgaris*).

In contrast, chipmunks (small ground squirrels) can utilize a flexible hoarding strategy, using both larder and scatter hoarding. This is possible because of two physiological adaptations: cheek pouches and hibernation. A chipmunk can economically collect a large number of small seeds in its cheek pouches, while a larger tree squirrel cannot. This allows chipmunks to construct multiple scatter hoards from a pouch load or deposit the entire load into a defended larder. Chipmunks further reduce their winter energy budget, compared with that of tree squirrels, using hibernation. However, this strategy also has consequences as hibernation is correlated with smaller brain size in mammals (Heldstab et al., 2018).

Hoarding decisions also can be directly influenced by physical factors such as atmospheric humidity, which impacts the accuracy of olfactory search and cache retrieval. A search dog's detection of a faint target odor was significantly more accurate in a warmer, more humid atmosphere (Jinn et al., 2020). Thus, while wild North American yellow pine chipmunks (*Tamias amoenus*) will pilfer caches in dry soils, they will pilfer more of their competitors' caches when the atmosphere is more humid (Downs & Vander Wall, 2009). In China, captive Siberian chipmunks (*T. sibiricus*) caching in a humid atmosphere will preferentially pilfer other's caches before retrieving their own (Yi et al., 2016). Olfaction's role in cache retrieval can be experimentally manipulated. When a native scatter-hoarding rat species is made experimentally anosmic in captivity, they shift retrieval strategies from olfactory search to relying on spatial memory (Yi et al., 2021).

Another influence on hoarding behavior that may be adapted to the physical environment is personality, defined as consistent among-individual differences in behavior across time and contexts. More heterogeneous habitats should select for greater variation in behavioral phenotypes (Mortelliti & Brehm, 2020). In wild food-storing deer mice (*Peromyscus maniculatus*), personality predicts a suite of foraging and hoarding decisions, including its persistence in search and whether a seed is eaten or cached (Boone et al., 2021). In wild Eurasian red squirrels, the survival value of being bolder or shyer varied among habitats: bolder squirrels survived longer when food supplies were unpredictable but shyer squirrels survived longer in habitats where food was stable. Boldness had fitness consequences for both females and males, and the more successful personality depended on resource abundances (Santicchia et al., 2018; Wauters et al., 2021). Similar results might be expected in wild larder-hoarding North American red squirrels, which inhabit not only coniferous but also deciduous forests. This shifts their

socioeconomics to a mixed strategy of larder and scatter hoarding (Mazzamuto et al., 2020), a flexibility of strategy that may well be influenced by personality.

The social environment

No squirrel is an island — hoarding and reproductive strategies are heavily influenced by social factors, even in apparently asocial species. To fill and then to defend its ‘central bank’, a larder hoarder faces social challenges on which its survival and reproductive success depend. Fitness is relative and the economics of larder hoarding is highly sensitive to social competition. Although solitary, the reproductive fitness of a red squirrel will be influenced by the social environment surrounding their larder. For example, when spruce cones are scarce, a wild red squirrel has lower reproductive fitness if surrounded by highly successful neighbors, though not when cones are abundant (McAdam et al., 2021). Squirrels must therefore closely monitor social relationships with known individuals to minimize time budgets for defense and vigilance. Wild red squirrels monitor neighbors through their rattle calls, a vocal advertisement used in territory defense. Squirrels can recognize the rattle calls of individuals, and those surrounded by unrelated but familiar neighbors are less vigilant. This ‘dear enemy effect’ results in squirrels expending less energy on territorial defense, which has positive fitness consequences (Robertson et al., 2018; E. Siracusa et al., 2017; E. R. Siracusa et al., 2019, 2021). Squirrels also use neighbor territorial calls as a proxy for competitor density. As density increases, squirrels initiate breeding earlier in the year, allowing their offspring more time to grow before independence (Fisher et al., 2017; Fisher, Wilson, et al., 2019). Wild red squirrels also reduce litter size when social competition is high, which increases pup growth rate and competitive ability (Dantzer et al., 2020). Finally, the social environment may also lead to altruism: if a lactating mother is killed, a female kin member may rescue, adopt and raise some of her orphaned pups (Gorrell et al., 2010).

The social environment is also critical to the midden acquisition and hoarding behavior of juveniles. A juvenile North American red squirrel must establish its own territory, fill its midden, and defend both from intruders to survive. Squirrels that acquire a territory before the fall crop ripens are more likely to do so (Hendrix et al., 2020). Territories can be taken over following the deaths of territory owners. Older males have larger middens and the usurper of their midden after their death will breed earlier and achieve higher reproductive fitness (Fisher et al., 2019). Offspring can also inherit a midden from kin: red squirrel mothers may even abandon their established territory to bequeath it to a daughter (Fisher et al., 2017). Thus, the economic food-storing decisions of one individual can have fitness consequences for other squirrels.

Personality also influences social interactions and hoarding behavior (Santicchia et al., 2020). Wild North American red squirrels show trajectories of individual differences in personality that are heritable and stable across an individual's lifetime (Martinig et al., 2020). These differences interact with social competition and the physical environment: the offspring of more aggressive females are more likely to survive in years when there is greater social competition for physical resources (Taylor et al., 2014). Finally, red squirrel mothers who are more attentive raise faster growing pups who achieve higher lifetime reproductive fitness (Westrick et al., 2020).

Scatter-hoarding squirrels adjust their caching behaviors in response to their social surroundings (Hopewell & Leaver, 2008; Leaver et al., 2006). Wild eastern gray squirrels employ 'evasive' tactics when caching food in the presence of others by adjusting the spacing of their caches and orienting their backs towards other nearby squirrels (Leaver et al., 2006). Moreover, as the number of conspecifics in a foraging patch increases, the rate at which squirrels

return to a patch between caches increases, indicating that competition decreases the energy expenditure on caching per item (Hopewell & Leaver, 2008).

In contexts where climate and resources are more variable, it may be more economically beneficial for hoarders to maintain a mixed hoarding strategy. Like chipmunks, captive kangaroo rats also have cheek pouches and show flexible hoarding strategies, adapting cache distribution in response to pilfer risk (Preston & Jacobs, 2001, 2005). Captive Siberian chipmunks shift caching strategy when detecting the sound and/or sight of a conspecific caching. The observer then increases its search for another's caches, which it then both scatter and larder hoards (Niu et al., 2019), though in other contexts, pilfered seeds are more likely to be larder hoarded (Yang & Yi, 2018). Wild scatter-hoarding Cape ground squirrels are not only sensitive to the presence of a conspecific but also to the conspecific's attentive state. Squirrels cache more when other squirrels are momentarily less attentive to their behavior (Samson & Manser, 2016).

The economics of risk

Hoarding entails two categories of existential risk: loss of life to predation and loss of caches, either to competitors or memory loss before retrieval. These risks differ among the three hoarding strategies (Figure 1.1). Larder hoarders theoretically face the least risk of cache loss via either pilfering or forgetting (Donald & Boutin, 2011; Jacobs & Spencer, 1994). Scatter hoarders must weigh the additional trade-off between predation and pilferage, as caches are more vulnerable where competitors can search more safely. Additionally, those deploying a mixed strategy must actively track the changing risks and benefits posed by scatter hoarding or larder hoarding in a given context and adjust decisions accordingly.

Predation and pilferage risk together shape hoarding strategy. Wild eastern gray squirrels cache preferred foods in open habitats where the predation risk is greater and pilferage risk is lower, while caching less preferred foods under the safety of the canopy (Lichti et al., 2017; Steele et al., 2014). In England, wild eastern gray squirrels were found to make these decisions based on prior heuristics rather than dynamic cues indicating current risks (Leaver et al., 2017) and in China, Siberian chipmunks also preferentially cached in open forest gaps (Yang et al., 2016). Here again, the physical and social environment shape the hoarding strategy.

Increases in space use increase the risk of predation (Steele et al., 2014, 2015). Arboreal scatter hoarders potentially face higher predation pressure than arboreal larder hoarding species, as they must forage, store, and later retrieve caches from much larger spatial areas. While scatter hoarding on the ground, they must also escape terrestrial predators. On the ground, wild eastern gray squirrels quickly calculate the distance of potential trees and the angular degree between the squirrel, predator, and tree when choosing escape routes (Eason et al., 2019). While foraging in trees, they must escape pursuit by flying and arboreal predators, such as owls, hawks, and small carnivores, such as pine martens (Twining et al., 2020). On rods of different diameters, captive eastern gray squirrels increase half-bounds and galloping as the branch diameter decreases (Dunham et al., 2019). Wild fox squirrels can adapt their launch position and force to the changing compliance of the launch branch while also maintaining the flexibility to incorporate parkour maneuvers to add additional control points mid-leap (Hunt et al., 2021). To further manage risk, wild eastern gray squirrels eavesdrop on bird chatter (Lilly et al., 2019).

The next risk emerges from the social environment — a scatter hoarder must combat loss of caches by employing strategic caching, deciding what to eat, what to cache and where to cache it. Captive eastern gray squirrels decide what seeds to eat or cache not by seed species but

by a combination of seed traits. They also chose to cache seed species that they had not already cached, increasing the nutritional diversity of stored foods (Sundaram et al., 2018). In the field, wild fox squirrels assess nut weight using specialized paw and head movements (Preston & Jacobs, 2009). Fox squirrels then invest effort proportionately to nut value, carrying heavier nuts farther and caching preferred nuts at lower densities (Delgado et al., 2014). Squirrels must also strategically place stored items to mitigate the risk of forgetting the cache location. Wild scatter-hoarding Cape ground squirrels employ a sun compass to orient both during caching and retrieval, to reduce this risk (Samson & Manser, 2016). Wild fox squirrels employ the mnemonic strategy of spatial chunking. Such a hierarchical organization of cached food items (e.g., spatial segregation of caches by nut species) should theoretically improve recall, based on studies in laboratory rodents. Given a pseudorandom series of different nut species, fox squirrels organized the scatter hoards into species-specific clusters (Delgado & Jacobs, 2017). Studies of captive Siberian chipmunks also reveal the potential risk of memory loss with males more likely than females to place caches near tall vertical landmarks (Zhang et al., 2016). Such a sex difference could emerge from the female advantage for spatial array memory, as in wild scatter-hoarding fox squirrels and captive kangaroo rats (Barkley & Jacobs, 2007; Waisman & Jacobs, 2008).

These examples capture only the initial decision of cache placement. In the field, radio-tagged acorns, presumably cached by wild eastern gray squirrels, were moved several times after initial caching. Hence, many studies probably underestimate the complexity of a scatter hoarder's strategy as such recaching would create a more recent memory of the cache's location (Bartlow et al., 2018). As squirrels continually deplete their caches, such recaching may also allow the squirrel to rearrange its remaining caches to optimize the dispersion of nuts to reduce cache pilferage by its competitors.

Thus, in physical environments where larder hoarding is not an economic option, squirrels must suffer the multiple increased risks of scatter hoarding (e.g., predation, forgetting, and pilferage). In chipmunks, these risks can be managed flexibly according to context and physical environment. During the summer, wild North American yellow pine chipmunks range more widely in space, scatter hoard seeds and do not defend a larder. As winter approaches, the chipmunks transport and concentrate their scattered caches as a larder in their hibernaculum. The wild Siberian chipmunk, which relies heavily on scatter hoarding during nonhibernating months, will also larder hoard when costs and benefits shift. In captivity, a Siberian chipmunk experiencing high rates of cache loss from its larder will shift to scatter hoarding (Wang et al., 2017). After pilfering, a captive chipmunk will store pilfered seeds in its larder (Yang & Yi, 2018). This may reflect the energetic value of a pilfered item, which may be counted as higher value as the owner, not the pilferer, paid for the initial search and handling costs.

The risk of cache loss due to pilfering also entails other species. Wild yellow pine chipmunks hoard in competition with other sympatric scatter hoarding species, including another chipmunk species and deer mice. All three of these species engage in reciprocal pilfering (Vander Wall & Jenkins, 2003), losing approximately 30% of their caches to hetero-specific pilferers. At the same time, all three species pilfer from the larders of the larger golden-mantled ground squirrel (*Callospermophilus lateralis*), which neither scatter hoards nor pilfers (Dittel et al., 2017). This is also seen in studies from China, where in the field and in captivity scatter-hoarding rodent species are more efficient cache pilferers than larder-hoarding species (Wang et al., 2018).

Conclusion

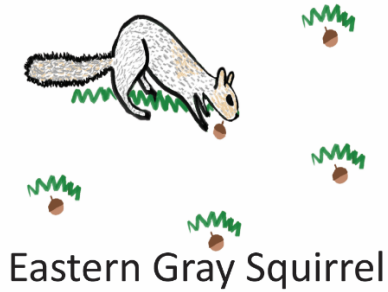
Hoarding strategies emerge from the affordances of the physical environment, in particular the adaptations of plants to reduce seed predation. These properties dictate the spatiotemporal distribution of surplus food, limiting the hoarding strategies that a squirrel can economically sustain. These physical factors in turn constrain the social environment, which is predicated on the need to reduce the risks of predation and cache loss (Figure 1.2). Squirrel cognition in the wild appears adapted to minimize risks, such as showing innovative motor learning during locomotion. Other losses — memory loss and pilfered caches — are driven by social competition, which may select for further cognitive traits, such as the ability to orient to celestial cues or to create a hierarchical organization of caches. Hoarding is thus a context-specific response to diverse factors — physical, social, and economic.

The impact of the interaction amongst the physical, social, and economic environments on behavior and cognition is evident across the food-hoarding strategy continuum (Figure 1.1). The packaging of conifer seeds in cones, where scale debris creates a long-term repository for seeds, creates a context where a nonhibernating tree squirrel can economically defend a territory, even surviving years where no cones are produced. The ability to defend this central bank then reverberates into adaptations for social competition among neighbors and within kin lineages. In contrast, the packaging of seeds by deciduous masting trees into acorns and nuts precludes this hoarding solution and instead instigates the information economy of the nonhibernating scatter hoarder. Because scatter hoarders are both predators and seed dispersers, this plant–animal relationship has led to the coevolution of seed morphology and squirrel cognitive traits necessary to assess, invest, and profit by their hoarding investments. Scatter hoarding also greatly increases the need to monitor and respond to social competitors. The costs of social competition, and its

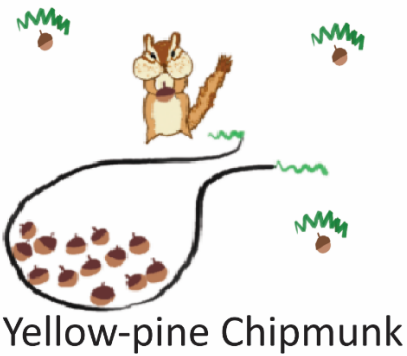
impact on hoarding decisions, are even more prominently displayed in the mixed strategy hoarding of chipmunks. Here, too, the physical environment — the need to use scatter hoards to prepare a larder hoard for winter hibernation — is critical to understanding the chipmunk’s social environment. And this in turn drives the cognitive traits required by such a mixed strategy.

As squirrels continue to adapt themselves to the human landscape, the study of hoarding offers the potential to understand how socioeconomic decisions flexibly adapt to new physical and social environments. It offers a unique opportunity to study perception, motor learning, spatial memory, and decision making in diurnal wild rodents. Urbanization is a potent selective force on wild squirrel behavior and cognition, where complex differences in response to cognitive challenges emerge between rural and urban squirrels, and native versus introduced squirrel species (Chow, Clayton, et al., 2021; Chow et al., 2018; Chow, Uchida, et al., 2021; Uchida et al., 2019). Hoarding strategies in such squirrels can be studied to tease apart the selective pressures arising from the physical and social environments. Thus, future studies of cognition in the wild of even a city squirrel, living in our increasingly cosmopolitan and carpentered world, can contribute significantly to our understanding of the evolution of socioeconomic behaviors.

Figure 1.1: The food-hoarding strategy continuum. Placement of caches exists on a continuum anchored by two extremes: scatter hoarding and larder hoarding. Acorns on the right represent the distribution of stored food items in space ranging from singular scattered caches dispersed across the landscape to defended larders clustered in one location. Illustrations to the left of the listed strategies show exemplar species known to deploy each strategy (top: eastern gray squirrel, middle: yellow pine chipmunk, bottom: North American red squirrel.)



**Scatter
Hoarding**



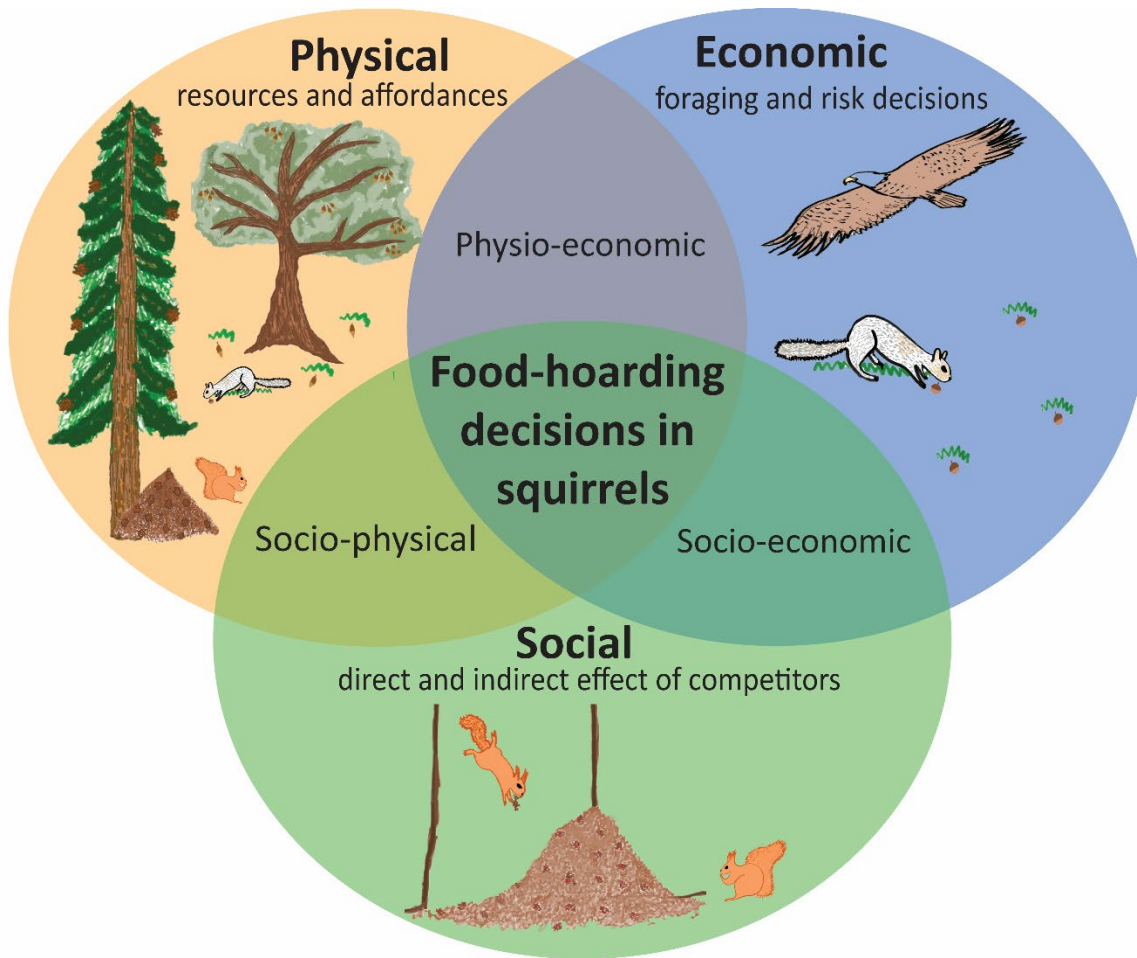
**Mixed
Strategy**



**Larder
Hoarding**



Figure 1.2: Wild squirrels are adapted for a diversity of complex food-hoarding economies. Food-hoarding decisions in squirrels account for the physical resources afforded by the environment, the economic decisions that require squirrels to exhibit suits of behaviors to reduce risks of predation and cache loss. Economic decisions in apparently solitary species are driven by social interactions.



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Chapter 2

Timely Investments: Environment and Experience Influences Food-Storing Decisions in Western Gray Squirrels (*S. griseus*)

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Abstract

Food-hoarding is a cognitively demanding task that requires individuals to account for competing variables to meet immediate and future needs. The first step in hoarding is the choice to eat or cache a found item. The eat-cache decision is influenced by a multitude of factors including satiety, food quality, competition, and predation risk. Overlaid onto these variables is the need to account for time at varying scales. This includes long term seasonal variations in environmental food abundance and the immediate energy needs of individuals that fluctuate throughout the day. As well as those learned through experience such as time already allocated to eating and storing and the time until a stored item is no longer viable. This work explores the influence of these considerations on the eat-cache decisions of a marked population of free living western gray squirrels (*Sciurus griseus*). As an obligate scatter-hoarding species their survival is dependent upon making thousands of eat-cache decisions yearly. Squirrels were provided access to a feeding station that presented a choice between an in-shell item suitable for storage and a minced item that must be eaten immediately. 3,198 eat-cache decisions were recorded from 34 individuals. Squirrels accounted for time of year, the number of decisions made previously, and item storability when deciding to eat or cache. Gaining insight into how *S. griseus* navigate a multitude of competing considerations when making food-storing decisions not only provides valuable insights into the complexity of their behavior but also sheds light on broader mechanisms likely underlying the flexible decision-making strategies of arboreal squirrels more broadly. This adaptability likely contributes to their groups' successful ability to adapt to the human landscape.

Introduction

To access enough food to survive and reproduce, animals must often deal with fluctuations of food availability across time. Long-term food hoarding species solve this problem by storing food in times of abundance. This turns a formally fleeting resource temporally concentrated at a singular seasonal time point, into a sustainable year-round life source (Robin & Jacobs, 2022). The first challenge faced by a food-storing individual is the ‘eat-cache’ choice to either immediately consume a found item or store it for future use. Animals must balance maximizing total storage while meeting immediate energy needs. For tree seed storing species, choosing to eat or cache is moderated by the interaction of a number of factors including satiety, food quality (e.g. seed size, fat content, tannin levels), social competition, and risk of pilferage (Jansen et al., 2004; Preston & Jacobs, 2009; Sundaram et al., 2018).

Critical to the success of a food-hoarder is effective time management at multiple scales. At its broadest level, hoarding behavior fluctuates throughout the year seasonally as the environmental availability of food and daylight shifts (MacDougall-Shackleton et al., 2003; Steele & Koprowski, 2001; Thompson & Thompson, 1980; Vander Wall, 1990). Changes in both photoperiod and food abundance associated with seasonal change can drive food-storing behavior (Steele & Koprowski, 2001; Vander Wall, 1990). During seasons of abundance, preference for storable items should increase in preparation for predictable seasonal shifts that result in food becoming scarce. (Delgado et al., 2014; Kuhn & Vander Wall, 2008; Steele & Koprowski, 2001; Vander Wall, 1990). Preference for consuming more easily accessible non-cacheable items alternatively should increase directly after periods of scarcity, as individuals may have decreased in body weight after relying on stored food for extended periods of time. However, individual decisions may deviate from these predictions based on sex and age (Kuhn &

Vander Wall, 2008). For example, during breeding seasons females may have higher food intake needs and prioritize eating more than would be expected based on seasonal food availability (Humphries & Boutin, 1996; MacWhirter, 1991). On a finer scale, time of day may influence the value individuals place on potentially storable items. For example, decisions in the morning with a hungry animal and a full foraging day still to come may differ from decisions made at the end of the day when future benefits may outweigh reduced immediate needs (Waite & Ydenberg, 1996). The impact of time of day on decisions may vary across seasons. For example, when food is abundant and animals may be at their highest weights of the year in preparation for scarcity, future benefits of storing may remain consistently high throughout the course of the day. This may differ in comparison to seasons with intermediate or low food availability when immediate energy needs may be higher overall following times of scarcity and in support of breeding.

Food-hoarders must choose foraging strategies that result in enough stored food for future survival while also compensating for the energy expended during the process of hoarding (Waite & Ydenberg, 1996). To accomplish this, individuals must balance how much time it takes to eat or cache with how much time they have already devoted to each activity. For example, eastern gray squirrels (*Sciurus carolinensis*) preferentially cache items that take longer to eat - even if those items are not as ideal for storage (Jacobs, 1992). Further, the eat-cache decision outcomes of eastern fox squirrels (*S. niger*) have been observed to be impacted by the amount of food an individual has already encountered (Delgado et al., 2014). Hoarders must also consider an item's storability, or the duration of time a given food item will remain viable if stored (Kotler et al., 1999). The perishability hypothesis predicts that eat-cache decisions are in a large part governed by an estimation of potential depletion of energy and nutrients an item will incur while stored (Juhasz et al., 2018). Larger seeds with thicker shells will remain viable underground for longer

compared to smaller more thinly shelled seeds (Sundaram et al., 2015). *S. niger*, invest more effort in concealing caches of hazelnuts (*Corylus avellana*) due to their thick shell and high caloric value compared to the time invested in burying thinner shelled lower calorie peanuts (*Arachis hypogaea*) (Delgado et al., 2014). Another important storability factor is time to germination. Cached acorns can germinate within months (Lichti et al., 2017; Steele & Yi, 2020; Xiao et al., 2009). Therefore, an individual must also consider time to retrieval to ensure the item will be viable upon return.

These considerations do not exist independently and may interact to shape decisions. The level and pattern of foraging activity on a short time scale, such as daily activity cycles, as well as long-term periods such as seasons will affect an animal's chances of survival (Wassmer & Refinetti, 2016). Individuals may prioritize different factors while storing food at different times of year to maximize total energy gain not within a single day but across entire seasons. For example, squirrels appear to be consistent in what seed traits are preferred for storage, however they make seasonally dependent trade-offs between these traits to maximize hoard size (Sundaram et al., 2018). In the fall when the frequency of storable items increases, squirrels follow a time-minimization strategy in which items stored were those that cut down on handling time and allowed for increased storage.

We explored how different considerations impact the preferences for cacheable versus immediately edible food items in free-living Western gray squirrels (*S. griseus*). As an obligate scatter-hoarder who does not hibernate, *S. griseus* is an ideal model system for studying trade-off decisions in food-storing. Their survival is dependent upon making thousands of eat-cache decisions during seasons of food abundance. Squirrels had access to an automated feeding station that presented a choice between two items: an in-shell cacheable item and minced nuts that can

be easily eaten but are not suitable for storage. In the framework of this simple binary choice, we were able to measure preferences for cacheable versus non-cacheable food relative to the season, time of day, number of previous decisions, and food item storability (Table 2.1).

Methods

Study Animals

The data represent food-storing decisions from 34 western gray squirrels (male = 17, female = 17) a part of a 164-squirrel marked study population at the James San Jacinto Mountains Reserve within the San Bernardino National Forest in Southern California. Squirrels are marked using Nyanzol-D (American Color and Chemical Corporation, Charlotte, NC) and implanted passive integrated transponder (PIT) tags (BioMark, Bosie, ID) allowing for the identification and retesting of individuals.

The study area is made up of a mature relatively untouched mixed conifer and oak forest with high levels of canopy connectivity. The reserve is located at 1,626 meters in elevation and is an ideal place to explore food-storing as it experiences extreme seasons of environmental food scarcity. The area receives an average of over 66 centimeters of precipitation annually and freezing temperatures for extended periods of time in the winter months. Non-hibernating squirrels such as *S. griseus* residing on the reserve are faced with immense pressure to ensure their food hoards are adequate to survive.

Ethical note

This work was approved by the University of California, Los Angeles Animal Research Committee (ARC-2017-094), the Institutional Biosafety Committee (BUA-2017-282-007) and

the California Department of Fish and Wildlife, Sacramento, California, U.S.A (S-139200001-20314-001). Further, these protocols have also been approved by the University of California, Riverside Office of Research Integrity and Institutional Animal Care and Use Committee. Methods used for handling squirrels in the field are in line with those of the American Society of Mammalogists for the use of wild mammals in research (Sikes & the Animal Care and Use Committee of the American Society of Mammalogists, 2016). Squirrels were trapped using Tomahawk live traps and placed in cone-shaped, cloth handling bags to reduce the stress of the animals (Koprowski, 2002). Squirrels remained in the handling bag for processing (i.e. obtain mass and sex) and marking and then were released at the location they were trapped. Squirrels on average were held for approximately 5-minutes, but never longer than 20-minutes. A 12mm pre-loaded needle system with Quick Eject Trigger from Biomark was used (Biomark, Bosie, ID). Trapping occurred daily for two weeks each month April -September 2021. Traps were open at sunrise and checked every two hours until closure at sunset. Traps were closed early on afternoons with excessively high or low temperatures. On average each individual was recaptured twice across the 2021 field season (min number of captures per squirrel = 1, max number of captures per squirrel = 8). Individuals captured after PIT-tag and fur dye had been previously administered were weighed and released upon recapture.

Automated feeding station

An automated feeding station was used to collect food-storing decisions made by squirrels at the site without an experimenter present. The system consisted of a 12-inch by 24-inch rectangular PIT-tag antenna (BioMark, Bosie, ID) surrounded by several overhead cameras. Food items were placed in the center of the antenna such that a squirrel would have to enter the scanning radius of the antenna to obtain food. The electrical components of the system including

the antenna batteries and data logger were stored away from the feeding station in weather proofed containers and connected to the station by cables. This prevented wildlife from disrupting the data collecting computer while allowing free access to the food.

Cacheable and non-cacheable food items

The feeding station offered squirrels the choice between two food item types: (1) a cacheable item and (2) a non-cacheable version of the same item. The cacheable items were seeds with intact shells that could be easily carried off and stored. The non-cacheable items were the same seed type used in the cacheable portion but removed from their shell and minced. This is an equally preferred food in terms of nutritional quality but has been rendered both less storable and less time costly (i.e., there is no handling time associated with removing a shell if the squirrel wants to immediately eat the seed). Thus, if the individual's intention is to immediately consume the item it should choose the minced seeds. Whereas, if storage is a priority the individual would benefit more by choosing the unshelled item. During the summer the food items at the feeder alternated between hazelnut trials (inshell and minced) and peanut trials (inshell and minced) to test for potential differences in preferences due to item storability. Hazelnuts with their thick shells will remain viable stored underground for longer periods of time than thinner shelled peanuts and thus are expected to be perceived as being higher in storability than peanuts (Delgado et al., 2014). During all other times of year only hazelnut trials were performed.

Testing days

Data were collected over 5 two-week intervals between April 2021 and September 2021. The study area was divided into three distinct zones based on trapping success in previous years. The feeder was placed in each zone for 4 days during each trip. During testing days, the feeding station was placed out within 2-hours of sunrise and removed within 2-hours of sunset. Food at the feeding station was replenished approximately every two hours.

Video scoring

Videos recorded by the cameras at the feeder were edited into smaller files of approximately 2 hours each and scored by observers using Behavioral Observation Research Interactive Software (BORIS) v.7.10.5 (Friard & Gamba, 2016). Observers recorded when squirrels arrived at the feeder, the food item chosen by the squirrel, and whether the squirrel ate the item within view of the camera or took the item. Additionally, the squirrel's unique PIT-tag identification number was added to the recorded behavior by matching the time displayed by the clock at the feeding station to the timed scans collected by the PIT-tag antenna.

In total 107 video files were scored, equating to 217.25 hours of footage, representing decisions made over 36 days of testing. Each file was observed by at least 3 observers. Inter-rater reliability was run within BORIS amongst all observers for each video file using both Cohen's kappa (mean = 0.80, max = 0.98, min = 0.32, SD = 0.14) and Needleman Wunsch test of similarity (mean = 0.97, max = 0.99, min = 0.78, SD = 0.03). The two observers with the highest Cohen's kappa were then isolated and placed side by side and lined up based on time. All records between observers that did not match both in decision and subject were dropped from analysis.

Statistics

To test the effect of both environment and experience-based considerations on eat-cache decisions three Generalized Linear Mixed Effects models (GLMM) with a logit link function in the lme4 package in R v.4.4.2 were used. The choice to eat or take a food item was used as a binomial response variable and squirrel identity a random effect in all models. The first model explored the effect of seasonality. Fixed effects included season, time of day, number of decisions already made by an individual at the feeder that day, average seasonal weight, age, and sex. Three seasons were tested: spring (March - May), summer (June - August), and fall (September - November). Time of day was binned such that decisions recorded from 6:00 – 11:59 were labeled as morning, 12:00 – 16:59 afternoon, and 17:00 – 20:00 as evening. Weight is representative of the average weight of all gray squirrels captured during the season in which the decision was made. In these models age is a categorical variable in which squirrels were classified as either a juvenile or adult based on body size, reproductive status, and time within the marked population. In models testing for the influence of storability, season was removed from the fixed effects as peanut trials were only performed in the summer. In these models, food type (hazelnut or peanut) was considered a categorical fixed effect. For each of the models forward and backward stepwise comparison was used to select the best fit model based on AIC score. The top ten ranked models for each of the models can be found in Appendix S2.1, only the best performing models are presented.

Results

A total of 3,198 total eat-cache decisions were recorded. Of these, 69% of the decisions resulted in taking the storable food item and 30% resulted in eating either the non-storable or

storable food item. When separated by seed type, squirrels took 73% of storable hazelnuts away from the feeder and ate 26% of them (Figure 2.1). They took 41% of storable peanuts and ate 58% of them (Figure 2.1). When opting to eat squirrels chose to eat the in-shell item over the minced item 53.15% of the time in hazelnut trials and 66.29% of the time in peanut trials (Figure 2.2). Because squirrels ate the in-shell cacheable item at a nearly equal rate as the minced version of the same item, “eat” is used as one variable in all models with no distinction between the item type eaten (i.e., minced or in-shell).

What influences eat-cache decisions made across seasons?

2774 individual decisions collected from 34 individuals (average of 82 decisions per squirrel) across all three seasons were included in these models. The best fit model included the fixed effects of season, number of previous decisions, and time of day (Table 2.2a). The number of decisions already made by an individual in each day was a strong predictor of whether a squirrel would choose to eat or take an item, such that as the number of previous choices increased, the likelihood of taking a storable item away from the feeder increased (GLMM: $Z = 9.11$, $p = <0.0001$) (Figure 2.3). Season also predicted choice such that in fall squirrels were more likely to take cacheable items from the feeder (GLMM: $Z = 3.1$, $p = 0.0019$) (Figure 2.4). In the spring and summer squirrels were more likely to eat either food item, with the likelihood of eating being highest in spring (GLMM: $Z = -2.62$, $p = 0.009$) followed by summer (GLMM: $Z = -2.19$, $p = 0.028$). There was a small trend towards taking the cacheable item over eating in the evening (GLMM: $Z = 1.89$, $p = 0.059$) but overall, the time of day was not a significant predictor of behavior.

Is food-item storability predictive of the eat-cache decision?

When isolated to the 424 decisions made when low storability items (i.e., peanuts) were available at the feeder over the summer ($n = 27$ squirrels, $m = 12$, $f = 15$) the highest ranked model included sex and time of day as fixed effects, none of which were found to be significant predictors of a squirrel's choice (Table 2.2c). The 6th ranked model was the first to show significant predictors of choice and included sex, time of day, and age as fixed effects (Table 2.2d). Both sexes were more likely to eat, with the likelihood of eating being higher for males (GLMM: $Z = -247.7$, $p < 0.001$) than females (GLMM: $Z = -20.68$, $p < 0.0001$). Age also predicted decisions such that juveniles were more likely to take cacheable peanuts than to eat them (GLMM: $Z = 140.39$, $p < 0.001$) (Figure 2.5). Based on the lack of significant predictors in the first five ranked models and the marginal difference in AIC score ($\Delta < 2$) between the models it is appropriate to find the outcomes of the 6th ranked model reasonable for use in understanding the eat-cache decisions of squirrels during peanut trials while avoiding overfitting (Harrison et al., 2018). During the same time of year when high storability food items (i.e., hazelnuts) were available at the feeder, 966 decisions were made by 25 squirrels ($f = 11$, $m = 14$) and the highest ranked model included only time of day as a fixed effect and was not found to be a significant predictor of a squirrel's choice, however the overall trend was towards taking the cacheable item over eating (Table 2.2b).

Blended models included 1390 decisions, 424 decisions collected during the peanut trials and 966 decisions collected during the hazelnut trials performed in the summer. 29 subjects ($f = 13$, $m = 16$) each making on average 48 decisions are represented. The best fit model included seed type (peanuts or hazelnuts), number of previous decisions made, and an interaction between seed type and number of decisions as fixed effects (Table 2.2e). Season was not included in these

models as peanut trials were only conducted in the summer. In the model that included both hazelnut and peanut trials, peanuts were found to be a significant predictor of eating (GLMM: $Z = -3.64$, $p = 0.00027$). Hazelnuts did not impact the choice to eat or take items in this model. The number of previous decisions was a predictor of choice (GLMM: $Z = 5.97$, $p = 2.38e-09$). There was a significant interaction between the number of previous decisions and seed type, such that the number of peanuts a squirrel had previously handled in a day increased the likelihood of eating (GLMM: $Z = -2.29$, $p = 0.0034$) (Figure 2.6).

Discussion

When deciding to prioritize eating or caching, hoarding animals face the complex task of accounting for a multitude of competing factors. Overlaid onto these variables is the need to account for time at varying scales. Firstly, long term seasonal variations in environmental food abundance as well as the immediate energy needs of the individual that may fluctuate throughout the day. Further, those learned through experience such as time already allocated to eating and storing and the time until a stored item is no longer viable. The data collected at the feeding station illuminates the nuanced decision-making process of *S. griseus*, who demonstrated a consideration of multiple factors when making decisions. Seasonal variations played a pivotal role, with a clear shift in behavior from prioritizing cacheable items in the fall, coinciding with the peak availability of storable acorns, to a gradual increase in focus on immediate consumption in the spring and summer. Moreover, our results indicate that the number of previous decisions made in a day strongly predicted subsequent actions, shedding light on the pivotal role of experience in shaping individual hoarding strategies. Seed type and age further impacted decisions made at the feeder, with squirrels displaying a clear preference for food higher in storability. Age shaped these decisions, such that older individuals with presumably more food

storing experience more strongly deprioritized caching when low in storability items were available, while juvenile squirrels stored these items at higher rates. Taken together these findings highlight the interplay of environmental and experiential variables accounted for by *S. griseus* when food storing, revealing a sophisticated approach to balancing immediate and future needs.

In line with our predictions, season played a significant role in eat-cache decisions. Squirrels prioritized taking cacheable items in the fall, while concentrating on immediate consumption in the spring and summer. This is consistent with the availability of storable acorns at the field site, which reach a yearly peak in the fall before becoming increasingly scarce over winter (Koenig et al., 2014; McDonald, 1990). High abundance of food has been shown to trigger storing behavior in a variety of hoarding species in both laboratory and field settings (Vander Wall, 1990). Further, as the time to winter decreases the importance of putting away food for future use increases. The probability of taking a cacheable item away from the feeding station was lowest in spring, which could be attributed to squirrels' potentially overall depleted energy stores directly following the winter. Additionally, historical data on the species indicates breeding in late February through early March followed by 45 days gestation and 10 weeks of lactation (Carraway & Verts, 1994; Cross, 1969; Linders et al., 2004). Thus, decisions to eat over store in the spring may reflect the need by females for additional metabolic resources to support young. Despite these considerations however, we did not find any significant sex differences in eat-cache decisions. Spring may also be a suboptimal time for caching from a storability standpoint due to its temporal distance from the following winter. Items stored in the spring may not retain viability for the extended period between then and winter (Lichti et al., 2017; Steele & Yi, 2020), they would also require a more prolonged memory of the storage location (Bartlow et al., 2018),

as well as being more susceptible to pilferage (Vander Wall & Jenkins, 2003). Short term caches may not be as important at this time either as other food sources such as fungus and pine nuts may be more abundant during this time of year (Cross, 1969). In the summer months, squirrels were still more likely to immediately consume food items than to take cacheable items from the feeder, but the probability of doing so was lower than in spring. This small shift may be the result of increased short term food storage in which individuals become satiated and begin to store food to be retrieved later in the same day or within several days from storing due to an overall decrease in environmental food sources like fungus.

Food-storing animals need to balance immediate energy needs with future energy needs while foraging. As individuals come across more food, eat, and become satiated, they should start to prioritize storage. Results at the feeding station are consistent with this prediction in that the number of decisions made previously was a strong predictor of what a squirrel would choose to do next across all the models. Squirrels were significantly more likely to take storable hazelnuts from the feeder as the number of previous decisions made already that day increased. This may also be a demonstration of the rapid sequestration hypothesis in that individuals after eating may focus on moving found food away from where it is concentrated in the habitat to get as much as possible before the resource is discovered by competitors (Zhang et al., 2014). The impact of the number of previous eat-cache decisions can also be viewed on a seasonal level. In spring, when presented with the feeding station for the first time after a prolonged period of limited access to storable food and the number of previously handled food items low, immediate consumption may take priority. As the months progress and individuals acquire more experience handling storable food, priority may shift to taking cacheable items. This is consistent with findings that squirrels maximize energy across seasons versus within individual days

(Smallwood & Peters, 1986). Contrary to our predictions, time of day was not found to be a significant predictor of decisions made at the feeder. It may be that the number of food items previously handled in a day is a more reliable indicator for making eat-cache decisions than the time of day, as it is a potentially more flexible heuristic that can account for seasonal changes in food availability and daily variations in other important but less predictable variables, such as encountering a lower or higher quality food patch or experiencing an afternoon storm.

Items in shells are perceived to have higher future value than those without (van der Merwe et al., 2014). Further, those with thicker less permeable shells such as hazelnuts are preferentially cached over thinner shelled items (Delgado et al., 2014). In line with these findings, storability of the seed type available at the feeder played a crucial role in determining eat-cache decisions. Squirrels were far more likely to take in-shell hazelnuts away from the feeder than they were to take in-shell peanuts. This is consistent with other tests of the perishability hypothesis in which eastern grey squirrels were shown to prioritize caching of seeds perceived to be more storable even if they are associated with higher handling times (Hadj-Chikh et al., 1996; Jacobs, 1992).

Squirrels accounted for the storability of a food item and differentially invested time in storing and eating based on the number of previous decisions made that day. In the blended models which included seed type as a fixed effect, there was a significant interaction between seed type and the number of previous decisions already made. As the number of previous decisions made increased so did the likelihood of taking a cacheable hazelnut from the feeder. During peanut trials, as the number of previously made decisions increased the likelihood of taking a cacheable item away from the feeder decreased indicating a perceived drop in the future value of the less cacheable seed type over time. However, because peanut trials were not conducted throughout the year, there may be important seasonal differences in the prioritization

of storability in the eat-cache decisions missing from the data set. Further, while the feeding station recorded squirrels taking cacheable items from the feeder it is not confirmed that these items were being stored for future use. It is possible squirrels were taking the food away from the centralized feeder to consume elsewhere.

Overall squirrels were more likely to eat in-shell peanuts than to take them from the feeder for storage in a way consistent with the difference in storability between hazelnuts and peanuts. However, age was a significant predictor of eat-cache decisions made during peanut trials such that juvenile squirrels were more likely to take cacheable peanuts than to eat them in comparison to their adult counterparts. Both adult and juvenile squirrels chose to take cacheable hazelnuts at about the same rate, whereas, during peanut trials juveniles took more cacheable peanuts than adults. These findings potentially illuminate interesting aspects of the ontogeny of food storing behaviors within an individual's lifetime. Juvenile squirrels have less experience assessing food items for storability and may be naive to indicators of perishability. Further, younger individuals may have smaller hoards overall and be more inclined to store. Little is known about the development of caching behaviors. There is evidence for both innate aspects of food storing decisions (Steele et al., 2006) as well as those learned through experience and social observation (Muñoz & Bonal, 2008; Weigl & Hanson, 1980). The effect of age could alternatively be the result of social hierarchy in which younger animals are more likely to be displaced from the feeder than adults and therefore more likely to carry food items away from the feeder for consumption. However, if this were the case it would also be expected to see the same impact on age in hazelnut trials which was not found.

Squirrels are managing a multitude of factors across contexts to make optimal decisions. By prioritizing eating or caching based on based on time of year, storability, and the number of

decisions already made within a day, squirrels work to maximize both internal and external energy stores. The role of age in aspects of eat-cache decision presents an intriguing avenue for future research on the ontogeny of food-storing behaviors. Being a successful scatter hoarder is a cognitively intense job requiring the management of a multitude of variables. These findings demonstrate the ability of squirrels to account for time across multiple levels.

Beyond the flexible behaviors exhibited by *S. griseus*, our study offers broader implications for our understanding of animal decision-making in changing environments. The sophisticated strategies employed by these squirrels to navigate a complex interplay of environmental cues, internal energy demands, and learned experiences mirrors a broader trend of flexible responses to cognitive challenges observed among arboreal squirrel species facing fluctuating resource availability (Robin & Jacobs, 2022). Exploration of the remarkable plasticity in foraging behaviors and cognitive processes across diverse ecological contexts is critical to provide a foundation for comparative studies in the field of animal behavior to better understand how wildlife will respond to the pressures imposed by rapidly changing environments.

Table 2.1: Food item preference predictions for each temporal context being tested.

<i>Temporal Context</i>	<i>Prediction</i>
<i>Season</i>	In preparation for winter when food is scarce, preference for storable items will increase in fall. Preference for consuming more easily accessible non-cacheable items will increase in the spring, as individuals may have decreased body weight after relying on stored food over winter.
<i>Time of day</i>	Immediately edible food items will be preferred at the start of the day. As individuals become satiated preferences will shift towards storable food, with a return to eating close to evening.
<i>Number of previous decisions</i>	As the number of food items handled by individuals at the feeding station in a day increases so will the preference for storable food with lower handling times.
<i>Storability</i>	Food items with higher storability will be preferentially taken from the feeder for storage.

Table 2.2: Parameter estimates of the best GLMMs for each model set. (a.) hazelnut trials across all seasons (b.) hazelnut trials in summer only (c.) highest ranked peanut model by stepwise iteration (d.) 6th ranked peanut model, but first with any significant predictive variables. (e.) highest ranked storability model which includes peanut and hazelnut trials run in summer.




	FIXED EFFECT	ESTIMATE	STD. ERROR	Z VALUE	PR(> Z)
 HAZELNUT MODELS	(a.) Season- Fall (Intercept)	0.624408	0.201034	3.105978	0.0019
	Season- Spring	-0.35815	0.136667	-2.62063	0.00878
	Season- Summer	-0.2772	0.126005	-2.19991	0.02781
	Number of previous decisions	0.066217	0.007267	9.112554	< 0.0001
	Time of Day- Evening	0.302477	0.160325	1.886646	0.05921
	Time of Day- Morning	0.062113	0.128782	0.482307	0.62959
	(b.) Time of Day- Afternoon (Intercept)	0.3717512	0.30957568	1.200841	0.229813
	Time of Day- Evening	0.476954	0.28785988	1.656896	0.09754
	Time of Day- Morning	0.8583559	0.25036831	3.428373	0.000607
	 PEANUT MODELS	(c.) Sex- Female Afternoon (Intercept)	0.35621	0.472578	0.753759
Sex- Male		-0.8683	0.504304	-1.72177	0.0851
Time of Day- Evening		-2.78048	1.418946	-1.95954	0.05
Time of Day- Morning		-0.52097	0.337839	-1.54205	0.1231
(d.) Sex- Female Adult (Intercept)		-0.06516	0.00315	-20.6895	< 0.0001
Sex- Male		-0.77997	0.003149	-247.691	< 0.0001
Time of Day- Evening		-2.73514	0.003149	-868.588	< 0.0001
Time of Day- Morning		-0.48977	0.003149	-155.543	< 0.0001
Age- Juvenile		0.442073	0.003149	140.388	< 0.0001
 BLENDED MODELS		(e.) Seed Type – Hazelnuts (Intercept)	0.2982952	0.22104072	1.349503
	Seed Type - Peanuts	-0.843781	0.23161923	-3.64296	0.00027
	Number of previous decisions	0.0753299	0.0126196	5.96928	< 0.0001
	Test – Peanuts * Number of previous decisions	-0.076224	0.02604626	-2.92647	0.00343

Figure 2.1: Proportion of decisions made for each seed type. 2,774 total decisions were collected during hazelnut trials. Of those squirrels chose to take storable hazelnuts away from the feeder 73% of the time and ate at the feeder 26% of the time. 424 decisions were recorded during peanut trials with squirrels opting to take storable peanuts away from the feeding station 41% of the time while eating at the feeder 58% of the time.

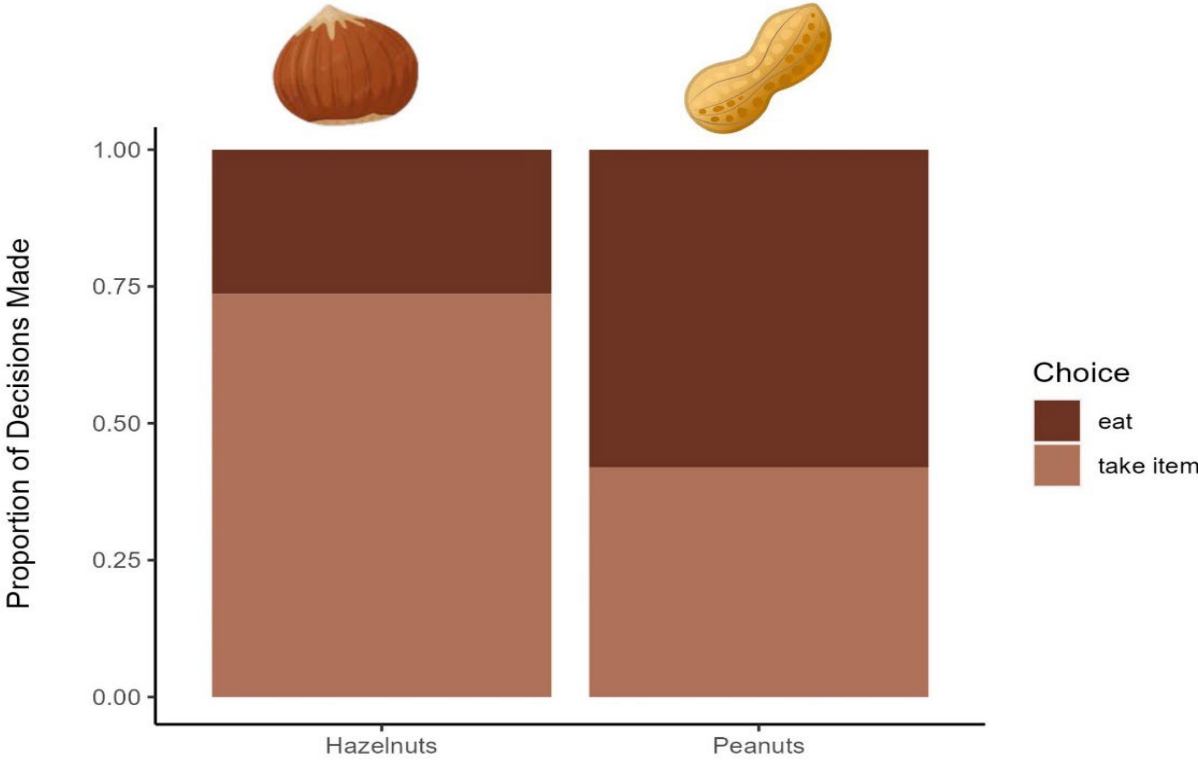


Figure 2.2: Proportion of item type eaten for each seed type. During hazelnut trials 53.15% of the time when choosing to eat squirrels opted to eat the in-shell storable hazelnut while choosing to eat the minced hazelnut 46.85% of the time. When eating during peanut trials, 66.29% of those chose to eat the in-shell item type and 33.71% opting for the minced peanut.

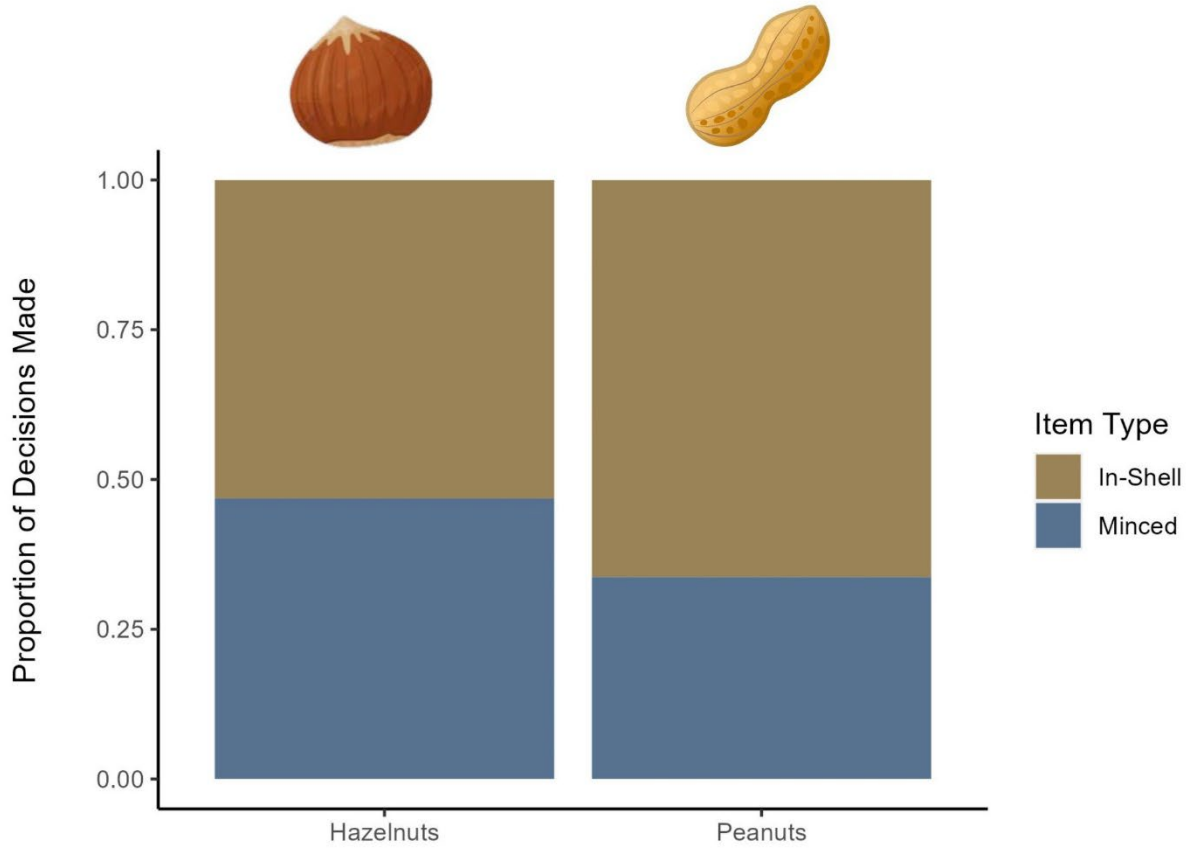


Figure 2.3: Proportion of cacheable items taken by number of previous decisions. The likelihood of taking a storable hazelnut away from the feeder increases as the number of previous decisions increases. Points indicate the percentage of all decisions to take the storable item made at that decision number across all squirrels and seasons. The line displays the mean predicted likelihood of taking the storable item at that decisions number as predicted by the highest ranked hazelnut model based on subsets of the data randomly sampled without replacement.

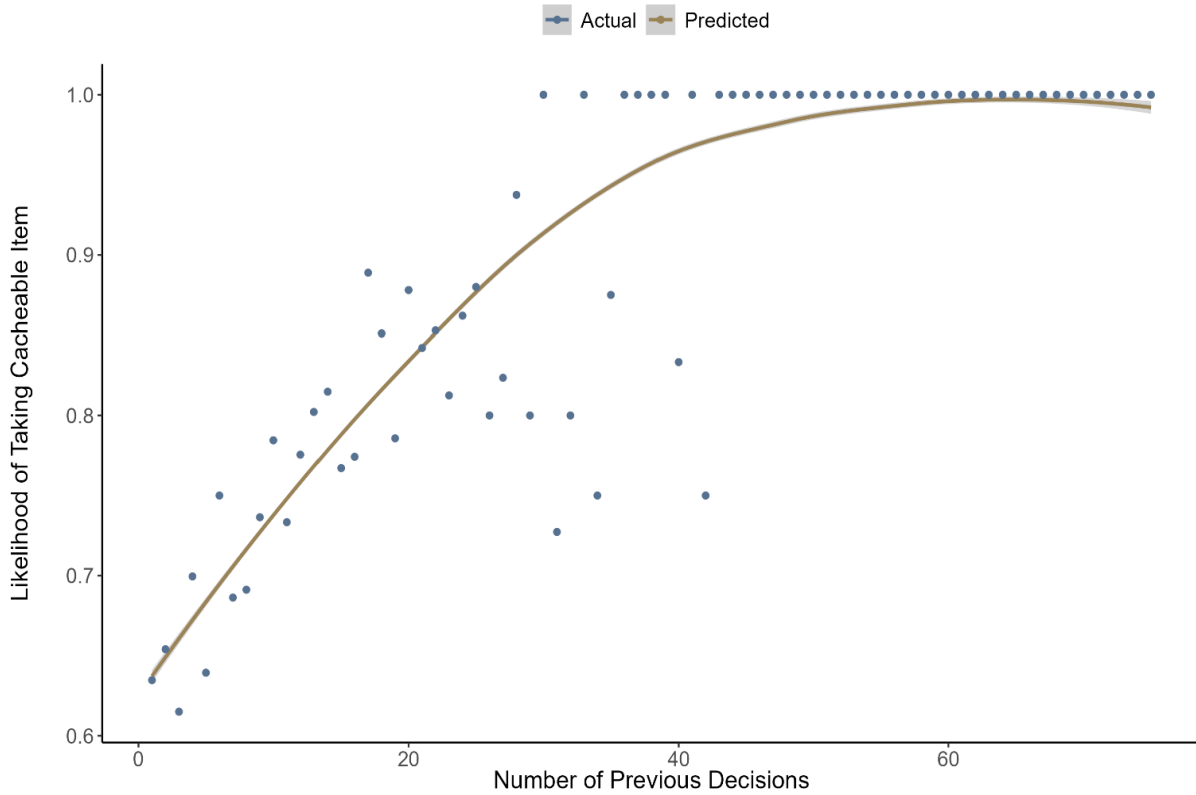


Figure 2.4: Proportion of take item decisions made by individuals per season. The proportion of total decisions to take storable items from the feeder per season was calculated for each of the 34 squirrels. Season was a significant predictor of eat-cache decisions. In the fall squirrels were more likely to select to take the storable item away from the feeding station ($\beta = 0.624$, $Z = 3.1$, $p = 0.0019$) in comparison to spring ($\beta = -0.358$, $Z = -2.62$, $p = 0.009$) and summer ($\beta = -0.277$, $Z = -2.19$, $p = 0.028$).

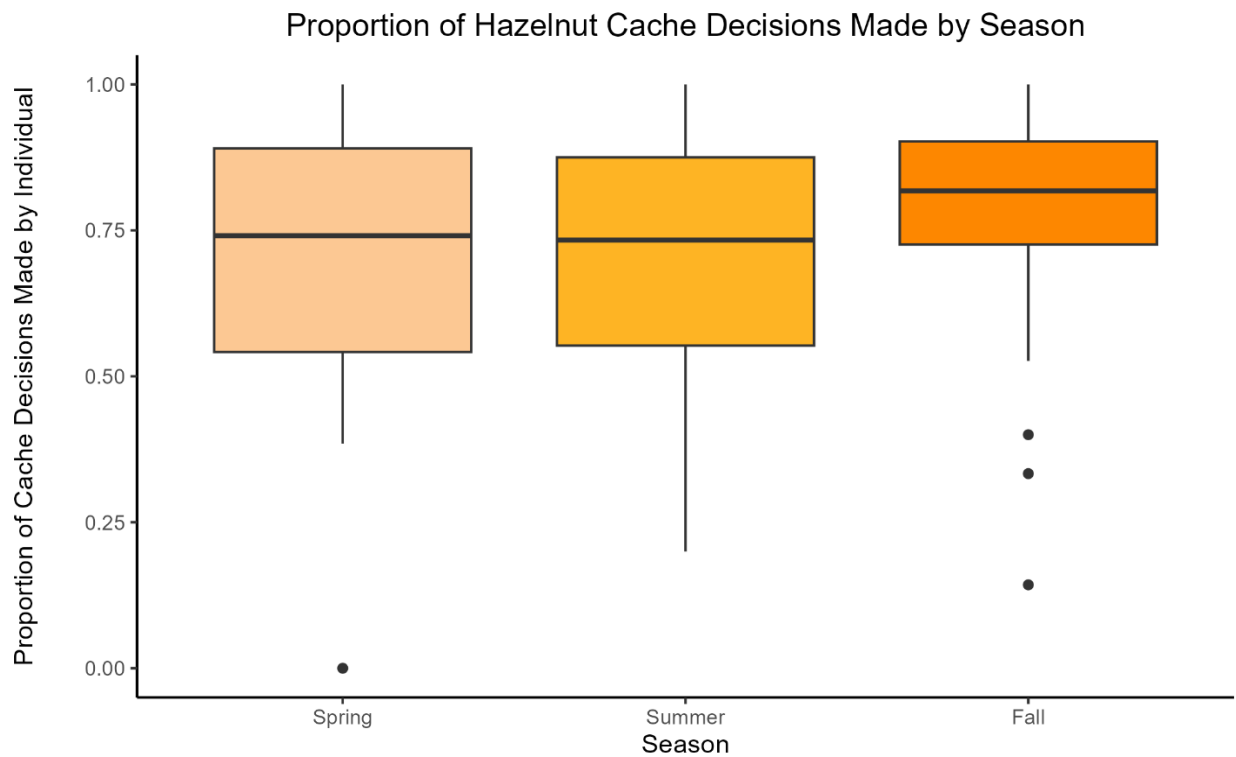


Figure 2.5: Proportion of decisions to take items made by squirrel age and seed type. The proportion of total decisions to take storable items from the feeder per seed type was calculated for each squirrel. Overall seed type was a predictor of decision. In the blended model squirrels were less likely to take storable peanuts from the feeder ($\beta = -0.844$, $Z = -3.64$, $p = 0.00027$). In the peanut models, age was a significant predictor of eat-cache decisions. Juvenile squirrels were more likely to select to take the storable peanut away from the feeding station in comparison to adults ($\beta = 0.442$, $Z = 140.39$, $p < 0.0001$).

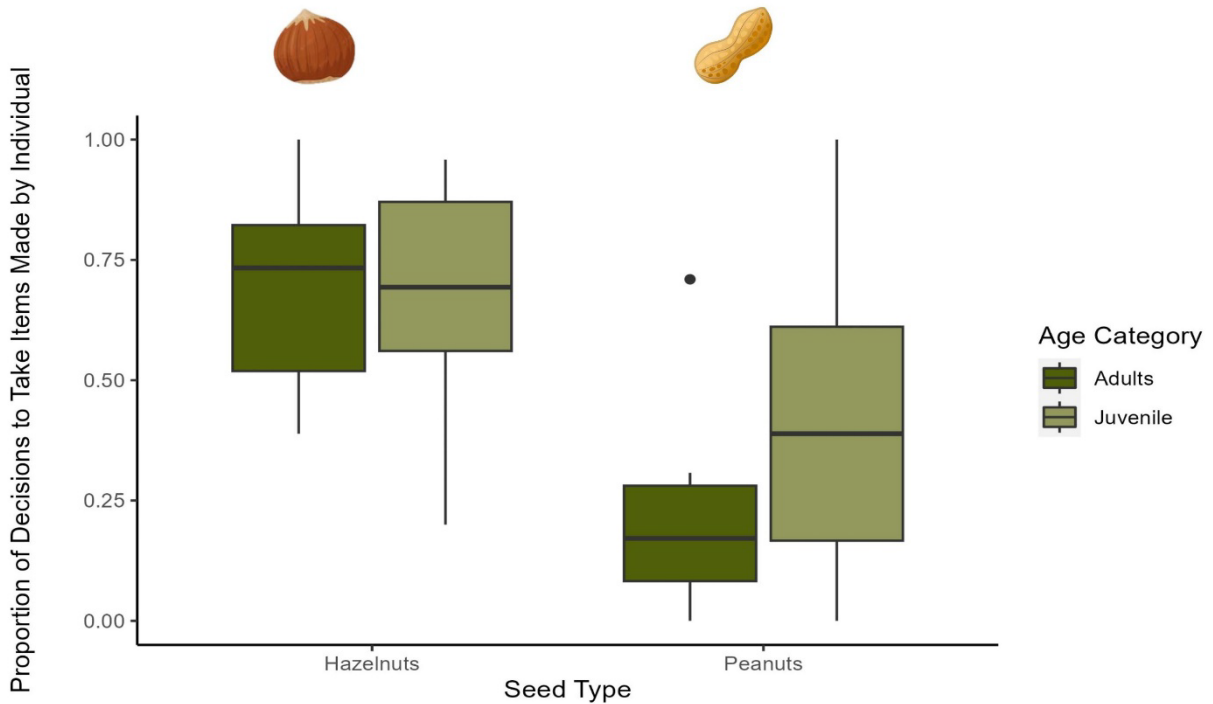
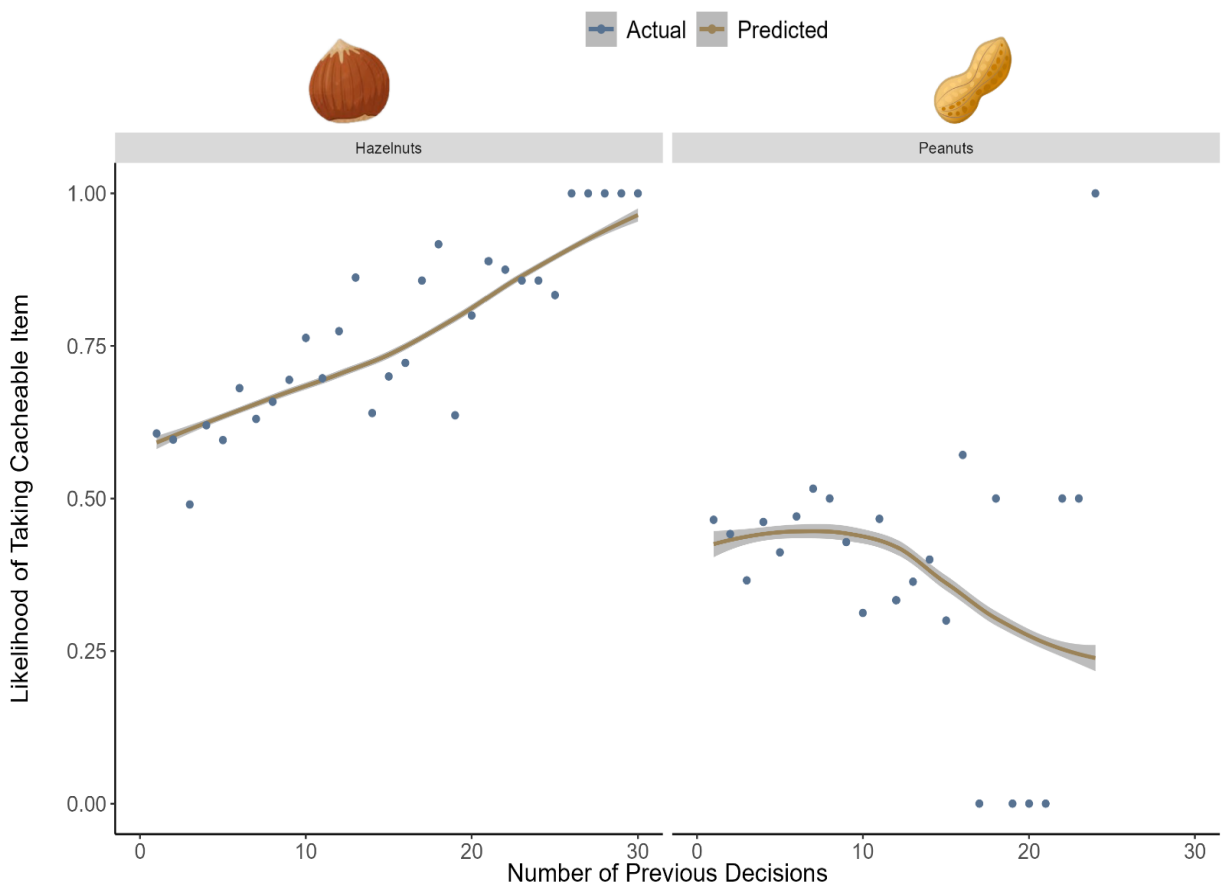





Figure 2.6: Proportion of cacheable items taken by number of previous decisions separated by seed type in the summer. During hazelnut trials, as the number of previous decisions a squirrel already made in a day increased, so did the likelihood of taking a storable hazelnut away from the feeder. During peanut trials, as the number of previous decisions increased, the likelihood of taking a storable peanut way from the feeder decreased. Points show the actual percentage of all decisions to take the storable item made at that decision number. The line displays the mean predicted likelihood of taking the storable item at that decision number as predicted by the highest ranked blended model based on subsets of the data randomly sampled without replacement.



Appendix S2.1: Selected variables and Akaike’s information criteria (AIC) values of top ten ranked models for each model set. ‘+’ indicates variable was included in model. (a.) hazelnut trials across all seasons (b.) hazelnut trials in summer only (c.) peanut models (d.) storability models (Rank ‘*’ best performing interaction model, outperforms highest ranked model).

	RANK	AGE	SEASON	SEX	WEIGHT	SEED TYPE	TIME OF DAY	NUMBER OF PREV.DECISIONS	LOGLIK	AIC	Δ AIC	WEIGHT
	1	(a.)	+			NA	+	+	-1434.03	2882.054	0	0.149887
	2		+			NA		+	-1436.11	2882.215	0.160763	0.13831
	3		+			NA	+	+	-1433.9	2883.792	1.737993	0.062858
	4		+	+		NA	+	+	-1433.9	2883.792	1.737993	0.062858
	5		+	+	+	NA	+	+	-1433.9	2883.792	1.737993	0.062858
	6		+			NA		+	-1435.99	2883.976	1.921589	0.057345
	7		+	+		NA		+	-1435.99	2883.976	1.921589	0.057345
	8		+	+	+	NA		+	-1435.99	2883.976	1.921589	0.057345
	9		+	+		NA	+	+	-1434.02	2884.037	1.983464	0.055598
	10		+	+		NA		+	-1436.1	2884.196	2.14231	0.051353
HAZELNUT MODELS	1	(b.)	NA	+		NA	+		-256.588	523.1752	0	0.087717
	2		NA	+	+	NA	+		-256.588	523.1752	0	0.087717
	3		NA			NA	+		-256.588	523.1752	2.96E-09	0.087717
	4		NA			NA	+		-258.03	524.0597	0.884486	0.056366
	5		+	NA	+	NA	+		-256.339	524.6781	1.502816	0.041376
	6		+	NA	+	+	NA	+	-256.339	524.6781	1.502816	0.041376
	7		+	NA		NA	+		-256.339	524.6781	1.502855	0.041375
	8		+	NA		NA	+		-257.456	524.9129	1.737675	0.036792
	9			NA		NA			-260.475	524.9498	1.774608	0.036119
	10			NA	+	NA	+	+	-256.492	524.9837	1.808422	0.035513
	1	(c.)	NA			NA		+	-530.833	1067.666	0	0.208348
	2		NA			NA	+	+	-529.284	1068.568	0.901227	0.132767
	3		+	NA		NA		+	-530.755	1069.511	1.844412	0.082848
	4		NA	+		NA		+	-530.832	1069.665	1.998448	0.076707
	5		NA	+	+	NA		+	-530.832	1069.665	1.998448	0.076707
	6		NA			NA		+	-530.832	1069.665	1.998448	0.076707
	7		+	NA		NA	+	+	-529.239	1070.478	2.81145	0.051085
	8			NA		NA	+	+	-529.281	1070.563	2.896448	0.048959

PEANUT MODELS	9		NA	+		NA	+	+	-529.281	1070.563	2.896449	0.048959
	10		NA	+	+	NA	+	+	-529.281	1070.563	2.896449	0.048959
 BLENDED MODELS	*	(d.)	Eat or Take Item ~ Seed Type + Seed Type * Number of Prev. Decisions + (1 Subject)					-801.4	1612.9	6.7		
	1					+		+	-805.839	1619.678	0	0.273404
	2		+				+		-805.504	1621.008	1.330372	0.140578
	3						+		-805.808	1621.617	1.939239	0.103682
	4				+		+		-805.808	1621.617	1.939239	0.103682
	5				+	+	+		-805.808	1621.617	1.939239	0.103682
	6		+				+		-805.503	1623.006	3.328215	0.051772
	7		+		+		+		-805.503	1623.006	3.328215	0.051772
	8		+		+	+	+		-805.503	1623.006	3.328215	0.051772
	9						+	+	-805.836	1623.672	3.994666	0.0371
	10				+		+	+	-805.496	1624.992	5.314699	0.19175

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Chapter 3

Shopping With Spectators: Exploring the Influence of Others on Eat-Cache Decisions

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Abstract

Long-term food-storing species transform seasonal surpluses into sustained resources, yet the risk of theft poses a crucial challenge. This dilemma arises as concentrated resources attract pilferers, intensifying competition. Even for solitary species with transient social bonds, food-storing decisions can be driven by social processes. One of the initial decisions a food-storer faces is whether a food item holds greater value stored or consumed. This work explores the influence of the presence of other squirrels on these decisions in a marked population of free living western gray squirrels (*Sciurus griseus*). As a solitary food-hoarding species their survival depends upon making thousands of eat-cache decisions yearly. Squirrels were provided access to a feeding station that presented a choice between an in-shell item suitable for storage and a minced item that must be eaten immediately. A significant majority of visits to the feeder occurred with just one squirrel present. Squirrels were least likely to overlap with others during times when food storage is known to increase such as in the fall, during the evenings, or when items are higher in storability. When interactions occurred, squirrels made adjustments in eat-cache choices. Squirrels favor cacheable items when: foraging alone; after displacing others; or in the presence of California ground squirrels (*Otospermophilus beecheyi*; heterospecific which does not store food). Overall, the results are consistent with reducing caching when potential thieves could observe the locations. Together these findings underscore squirrels' sensitivity to competition and the ability to integrate it into their eat-cache decision-making.

Introduction

Long term food-storing species transform a seasonal surplus of resources into a sustained year-round lifeline. However, investing time and energy in hoarding introduces several notable dilemmas: securing enough food to balance future and immediate energy needs, the threat of

spoilage before retrieval, and defense or memory of stored items. Layered on to each of these conditions is the threat of theft before retrieval. Hoarding concentrates resources within the environment which heightens social competition by attracting pilferers. Thus, even for solitary species, food-storing decisions may be shaped by the social environment (Jacobs, 2009).

Spanning a continuum, food-hoarding strategies range from larder hoarding, where food is protected in a single location, to scatter hoarding, depositing single undefended items across the landscape. The approaches deployed to mitigate this risk of pilferage are dependent on the food-storing strategy utilized. Multiple seeds bundled in a single cone and long germination times facilitates larder hoarding (Smith, 1968). Effective anti-pilfer strategies balance larder defense with acquiring more food (Robertson et al., 2018; E. Siracusa et al., 2017; E. R. Siracusa et al., 2019, 2021). Conversely, the availability of seeds from deciduous trees like oaks and hickories are less predictable and germinate faster, rendering them impractical to defend in a territory, leading to scatter hoarding across the landscape (Lichti et al., 2017; Steele & Yi, 2020).

The dispersed nature of their reserve presents scatter-hoarders with distinct challenges in protecting their cached food. Scatter-hoarding places heightened demands on the individual when: (1) deciding if a found food item has a higher value if eaten immediately or stored, (2) deciding where to store, and (3) recalling placement and retrieving items prior to spoilage or pilferage. Social competition is likely to influence food-storing decisions at each of these levels as these hoarders cannot engage in territorial defense and therefore must innovate other ways to counteract thievery.

Social competition shapes scatter hoarding strategies at the level of cache location selection and recall. Squirrels adjust their cache site selection behavior in response to competitors

(Hopewell & Leaver, 2008; Leaver et al., 2007; Samson & Manser, 2016a; Steele et al., 2008). Further, individuals may tolerate higher predation risks to counter pilferage, placing food farther from cover (Lichti et al., 2017; Steele et al., 2014, 2015). The competitive environment also influences the third challenge of remembering and retrieving items. Caches are not a static resource established and consumed, but rather, a dynamic food supply subject to ongoing reorganization (Vander Wall & Jenkins, 2003). Many species reposition items after an initial caching event, enhancing memory and reducing pilfer risk (Bartlow et al., 2018). Squirrels excel at recalling their caches, strategically placing items to minimize forgetfulness (Delgado & Jacobs, 2017; Devenport et al., 2000; Jacobs, 1992; Samson & Manser, 2016b).

Prior to deciding where to cache or remembering its location, a scatter-hoarder must navigate the decision to eat or store a found food item. To make this eat-cache decision, a hoarder must decide if the item has more value consumed immediately or saved for future scarcity. This choice is impacted by an interaction of environmental and state dependent factors. Animals must balance maximizing total storage while meeting immediate energy needs (Wassmer & Refinetti, 2016). For arboreal squirrel species, choosing to eat or cache has been demonstrated to be moderated by the interaction of a number of factors including season, time of day, number of previous eat-cache decisions already made, satiety, food quality (e.g. seed size, fat content, tannin levels), and risk of pilferage (Robin et al, in prep, Jansen et al., 2004; Preston & Jacobs, 2009; Sundaram et al., 2018). The influence of social competition at this junction in the food storing process is less clear. Work with food storing birds finds that the increased presence of others at the eat-cache decision can lead to increased consumption and a reduction or cessation in caching (Dally et al., 2006). While other species, such as the white-footed mouse (*Peromyscus*

leucopus), showed an increase in caching in the presence of others as a possible countermeasure against cache loss (Dally et al., 2006; Sanchez & Reichman, 1987).

To understand the impact of competitive interactions on eat-cache decisions of solitary foragers, it's crucial to first assess the level of social competition in a foraging patch and consider how environmental factors like season and time of day may moderate it. Seasonal variations in food availability and daylight significantly influence food-storing behavior (MacDougall-Shackleton et al., 2003; Steele & Koprowski, 2001; Thompson & Thompson, 1980; Vander Wall, 1990) and can also affect the frequency and outcomes of competitive interactions (Cross, 1969), which in turn may shape eat-cache decisions. For example, during breeding seasons with heightened interaction and increased food intake needs (Humphries & Boutin, 1996; MacWhirter, 1991), individuals may be more likely to tolerate the proximity of others while foraging. During these times when there are more potential pilferers present, immediate consumption may take priority (Dally et al., 2006). Conversely, in periods of food abundance when caching is a priority, competitive interactions may be less common. Additionally, the time of day can impact the likelihood of encountering an interaction and how the interaction may influence an eat-cache decision. For instance, in the morning, with a hungry squirrel and a full day ahead, immediate consumption may be prioritized (Robin et al, in prep), as such the presence of others may be more tolerated during times of day when storage is more likely to be prioritized.

The storability of a food item and the number of items already handled in a day may further influence the tolerance for social competition within a foraging patch. Storability refers to how long a food item remains viable if stored (Kotler et al., 1999). Larger seeds with thicker shells are higher in storability because they can remain viable underground for longer periods compared to smaller, thinly shelled seeds and as such have higher storability (Sundaram et al.,

2015). When low-storability items are present squirrels are more likely to prioritize immediate consumption (Robin et al, in prep). During this time the likelihood of interacting with others may be higher than during times when there is food with high future value and caching is prioritized. Additionally, the handling of a higher quantity of storable food items in a day may be associated with an increased tolerance for the presence of others due to behavioral discounting. The number of eat-cache decisions within a foraging session has been demonstrated to result in a reduction in the perceived value of items (Delgado et al., 2014). This decrease in value as more items are handled may allow for an increased acceptance of others while foraging.

Lastly, the composition of species competing at a foraging patch may impact the probability of competitive interactions occurring as well eat-cache decision outcomes. To prevent catastrophic cache depletion, scatter-hoarders must remain vigilant against both hetero- and conspecific pilferers. For example, yellow pine chipmunks (*Tamias amoenus*) lose a significant percentage of caches to heterospecific pilferers (Dittel et al., 2017). However, this may be further dependent on whether the heterospecific species is also a scatter-hoarder, as non-food storing and larder hoarding species have been shown to be less adept at pilfering (Dittel et al., 2017; Vander Wall & Jenkins, 2003; Wang et al., 2018). Nonetheless, it is estimated that the pilferage rate of a long-term scatter-hoarding individual is upwards of 30% of caches made per day (Vander Wall & Jenkins, 2003). For a scatter-hoarder, the energy invested in a cache is only recouped if the item is remembered and collected prior to spoiling or being pilfered.

Here we investigate the impact of competition on the first challenge faced by scatter-hoarders, the eat-cache decisions, in free-living western gray squirrels (*Sciurus griseus*). *S. griseus* is a solitary, non-territorial, obligate scatter-hoarding, arboreal squirrel species that does not hibernate. Their survival depends on making thousands of eat-cache decisions during seasons

of abundance to survive scarce winters. While many factors influence their decision making, we focus on (1) the impact of environmental variables (i.e., season and time of day) and those associated with experience (i.e., storability and amount of food handled) on shaping the number of competitive interactions an individual encounters and (2) how the outcome of these interactions subsequently shape the choice to eat or cache. This was investigated using an automated feeding station offering a choice between in-shell cacheable items and minced nuts unsuitable for storage. To measure the influence of both hetero- and conspecifics, we conducted our research in an area where *S. griseus* coexists with California ground squirrels (*Otospermophilus beecheyi*), a semi-fossorial socially living, non-food storing species.

The presence of others at the feeder while a squirrel forages may pose three problems for an individual: (1) opting to cache in the presence of others may increase the risk that the item will be pilfered, (2) caching will introduce an opportunity cost, where items at the feeder are depleted during absences, and (3) remaining at the station to consume shelled nuts may result in being disrupted by others. This experiment examines the trade-off that squirrels navigate between these conflicting challenges, investigating how considerations such as season, time of day, and food type might predict heightened competition at the feeder, the types of social interactions occurring at the feeder, and how these interactions may influence preferences for cacheable food items.

Methods

Study Animals

The data represent visits to the feeding station from 39 western gray squirrels (male = 19, female = 20) as part of a 164-squirrel marked study population at the James San Jacinto Mountains Reserve within the San Bernardino National Forest in Southern California. Squirrels

were marked using Nyanzol-D (American Color and Chemical Corporation, Charlotte, NC) and implanted passive integrated transponder (PIT) tags (Biomark, Bosie, ID) allowing for the identification and retesting of individuals.

Ethical note

This work was approved by the University of California, Los Angeles Animal Research Committee (ARC-2017-094), the Institutional Biosafety Committee (BUA-2017-282-007) and the California Department of Fish and Wildlife, Sacramento, California, U.S.A (S-139200001-20314-001). Further, these protocols have also been approved by the University of California, Riverside Office of Research Integrity and Institutional Animal Care and Use Committee. Methods used for handling squirrels in the field are in line with those of the American Society of Mammalogists for the use of wild mammals in research (Sikes & the Animal Care and Use Committee of the American Society of Mammalogists, 2016). Squirrels were trapped using Tomahawk live traps and placed in cone-shaped, cloth handling bags to reduce stress of the animals (Koprowski, 2002). Squirrels remained in the handling bag for processing (i.e., obtain mass and sex) and marking and then were released at the location they were trapped. Squirrels on average were held for approximately 5-minutes, but never longer than 20-minutes. A 12 mm pre-loaded needle system with Quick Eject Trigger from Biomark were used (Biomark, Bosie, ID). Trapping occurred daily for two weeks each month April -September 2021. Traps were open at sunrise and checked every two hours until closure at sunset. Traps were closed early on afternoons with excessively high or low temperatures. On average each individual was recaptured an average of 2 times across the 2021 field season (min number of captures per squirrel = 1, max min number of captures per squirrel = 8). Individuals captured after PIT-tag and fur dye had been previously administered were weighed and released upon recapture.

Automated feeding station

We used an automated feeding station to collect food-storing decisions made by squirrels at the site without an experimenter present. The system consisted of a 12-inch by 24-inch rectangular PIT-tag antenna (Biomark, Bosie, ID) surrounded by several overhead cameras. We placed food items in the center of the antenna so that a squirrel would have to enter the scanning radius of the antenna to obtain food. The electrical components of the system including the antenna batteries and data logger were stored away from the feeding station in weather proofed containers connected to the feeding station by cables. This prevented wildlife from disrupting the data collecting computer while allowing free access to the food.

Cacheable and non-cacheable food items

To explore the preference for items with future value versus those that cannot be stored and must be consumed immediately, the feeding station offered squirrels the choice between two food item types: (1) a cacheable item and (2) a non-cacheable version of the same item. The cacheable items were seeds with intact shells that could be easily carried off and stored. The non-cacheable items were the same seed type used in the cacheable portion but removed from their shell and minced. This is an equally preferred food in terms of nutritional quality but has been rendered both less storable and less time costly (i.e., there is no handling time associated with removing a shell if the squirrel wants to immediately eat the seed). Thus, if the individual's intention is to immediately consume the item it should choose the minced seeds. Whereas, if storage is a priority the individual would benefit more by choosing the unshelled item. During the summer, the food items at the feeder alternated between hazelnut trials (inshell and minced) and peanut trials (inshell and minced) to test for potential differences in preferences due to item

storability. Hazelnuts with their thick shells remain viable stored underground for longer periods of time than thinner shelled peanuts and thus were expected to be perceived as being higher in storability than peanuts (Delgado et al., 2014). During all other times of year only hazelnut trials were performed.

Testing days

We collected data over 5 two-week intervals between April 2021 and September 2021. We divided the study area into three distinct zones based on trapping success in previous years. The feeder was placed in each zone for 4 days during each trip. On testing days, we placed the feeding station out within 2-hours of sunrise and removed it within 2-hours of sunset. We replenished the food at the station approximately every two hours.

Social Interactions

Interactions between squirrels at the feeder were recorded via two channels. First, the PIT-tag scanner scanned for and recorded squirrel IDs continuously while turned on and recorded repeated IDs every 5-seconds. This allowed for the identification of instances of overlap between two PIT-tagged individuals at the feeder and for the calculation of the duration of that overlap. Squirrels were considered to overlap with one another when both PIT-tags were picked up by the antenna at the same time. On average squirrels must be within about 16 cm from the antenna to be picked up. Cameras recording videos later scored by observers allowed for the recording of the social outcome of the overlap between the two squirrels at the feeder and the eat-cache decision made (*see* Video scoring).

Video scoring

Videos recorded by the cameras at the feeder were edited into smaller files of approximately 2 hours each and scored by observers using Behavioral Observation Research Interactive Software (BORIS) v.7.10.5 (Friard & Gamba, 2016). Observers recorded when squirrels arrived at the feeder, the food item chosen by the squirrel, and whether the squirrel ate the item within view of the camera or took the item. The squirrel's unique PIT-tag identification number was added to the recorded behavior by matching the time displayed by the clock at the feeding station to the timed scans collected by the PIT-tag antenna. In total 107 video files were scored, equating to 217.25 hours of footage, representing decisions made over 36 days of testing. Each file was observed by at least 3 observers. Inter-rater reliability was run within BORIS amongst all observers for each video file using both Cohen's kappa (mean = 0.80, max = 0.98, min = 0.32, SD = 0.14) and Needleman Wunsch test of similarity (mean = 0.97, max = 0.99, min = 0.78, SD = 0.03). The two observers with the highest Cohen's kappa were then isolated and placed side by side and lined up based on time. All records between observers that did not match both in decision and subject were dropped from analysis.

These passed files then underwent additional analysis for social interactions between squirrels at the feeder. Two new observers were assigned to overlay scores for social behavior on to previously passed video files of eat-cache decisions at the feeder. To do so observers toggled to each "at feeder" behavior denoted in a BORIS observation file and using that squirrel as the focal individual denoted the presence of any social overlap between squirrels. Each social overlap behavior was labeled with a modifier that denotes the species of squirrel the focal individual overlapped with at the feeder and the outcome of that interaction. Possible social outcome modifiers included (1) displace- the squirrel originally at the feeder leaves as the focal squirrel

approaches, (2) stay- both the focal squirrel and squirrel originally at the feeder remain at the feeder together, (3) leave- the focal squirrel leaves the area upon noticing the squirrel originally at the feeder. The two socially annotated files were then lined up and any social behaviors that did not match between observers were dropped from the analysis.

Statistics

To explore what environmental conditions predicted overlapping between two squirrels at the feeder we used a Generalized Linear Mixed Effects model (GLMM) with a logit link function and a binomial family in the lme4 package in R v.4.4.2 . The presence of social overlap during the visit was the binomial response variable in these models (i.e., “yes social overlap present during visit” or “no social overlap present during visit”). Fixed effects included in the full model were season, previous number of visits to the feeder that day, time of day, sex, and food type, with subject as a random effect. Three seasons were tested: spring (March - May), summer (June - August), and fall (September - November). Time of day was binned such that decisions recorded from 6:00 – 11:59 were labeled as morning, 12:00 – 16:59 afternoon, and 17:00 – 20:00 as evening. Age in these models is a categorical variable in which squirrels were classified as either a juvenile or adult based on body size, reproductive status, and time within the marked population. Food type is included as a categorical variable representing the availability of hazelnuts or peanuts at the feeder during the visit. The top ten ranked models can be found in Appendix S3.1. The best performing model presented here included season, time of day, number of previous visits made in the day, and food type.

To test the impact of the environment on the duration of time two squirrels overlapped while foraging at the feeder we used a GLMM with a gamma link function. Gamma distributions

are commonly used for modeling positively skewed data such as durations of time (Helsler et al., 2004; Yeater, 2019). Forward and backward stepwise model comparison was used to select the best fit model based on AIC score. The top ten ranked models can be found in Appendix S3.1, only the best performing models are presented here. Fixed effects in the full model included the species the focal individual overlapped with at the feeder, season, time of day, number of previous visits to the feeder, the sex and age of the focal squirrel, and the food type available at the feeder. The top performing model only included the species of the squirrel the focal individual overlapped with at the feeder.

To assess the impact of social overlap at the feeder on eat-cache decisions, we utilized a Generalized Linear Mixed Model (GLMM) with a logit link function. The choice to either eat or take a food item was treated as a binomial response variable, while the presence of social overlap during the visit served as a categorical fixed effect, with subject as a random effect. Social overlap was represented as a binary variable, indicating whether another squirrel was present at the feeder during a visit (coded as ‘yes’ or ‘no’). For visits involving social overlap, we also included additional variables for overlap species and social outcome. Overlap species was defined as a categorical variable, indicating whether the squirrel overlapped at the feeder with a conspecific (*S. griseus*) or a heterospecific (*O. beecheyi*).

Lastly, to test the impact of the outcome of a social interaction on eat-cache decisions within the subset of 410 visits to the feeder that contained social overlap, a GLMM with a logit link function was used in which the eat or take a food item was a binomial response variable and the fixed effect was the categorical variable of social outcome. Social outcome is a categorical variable with three options (1) displace, (2) stay, or (3) leave describing the action taken by the

focal squirrel during the visit. Subject was included as a random effect in every model to account for repeated measures of individual squirrels.

Results

Are competitive interactions happening at the feeder?

A total of 8610 visits to the feeder by 39 squirrels (female = 20, male = 19) were recorded by the RFID antenna (mean visits per squirrel = 223.62, max number of visits = 659, min number of visits = 1, SD = 162.84). Mean duration of each visit was 71.29 seconds (max visit duration = 3082 secs, min visit duration = < 1 sec, SD = 127.67). Squirrels tended to forage alone, with 77% of all visits to the feeder occurring without overlap of other squirrels. The average time lapse between one squirrel leaving the feeder and another squirrel approaching was 20.83 minutes (max = 458.98 mins, min = 0, SD = 46.37).

In the 23% of visits that contained overlap between squirrels, 503 of them occurred with another gray squirrel, and 1,504 of the visits occurred with *O. beecheyi* (Figure 3.1). The presence of another squirrel at the feeder altered the average duration of the visit, however there was little difference between the visit duration during instances of overlap with heterospecific versus conspecifics. The average duration any two squirrels overlapped at the feeder was 1.30 seconds (min = <1 sec, max = 4 seconds, SD = 1.27). The best fit model to predict duration of the overlap included only the species with whom the focal gray squirrel overlapped with. When at the feeder with a heterospecific the duration of the overlap was predicted to be 93% shorter than when a gray squirrel was at the feeder (GLMM: $Z = -2.41$, $p < 0.0001$) (Table 3.1a).

Overlapping with another squirrel at the feeder was predicted by the season, number of previous visits, the time of day, and type of food available (Table 3.1b; Figure 3.2). Season

predicted the likelihood that squirrel visits would overlap at the feeder such that in fall squirrels were less likely to overlap (GLMM: $Z = -14.08$, $p < 0.0001$). In the spring and summer squirrels were more likely to overlap with one another while visiting the feeder (spring - GLMM: $Z = 5.90$, $p < 0.0001$; summer - GLMM: $Z = 7.56$, $p < 0.0001$). The number of visits already made by an individual in a day was also a predictor of whether a squirrel would overlap with others at the feeder, such that as the number of previous visits increased, the likelihood of overlap increased (GLMM: $Z = 2.07$, $p = 0.039$). Time of day also influenced potential overlap of squirrels during visits such that squirrels were less likely to overlap with others at the feeder in the evening (GLMM: $Z = -6.46$, $p < 0.0001$). Lastly, squirrels were more likely to tolerate overlap with others when peanuts were available at the feeder in comparison to the higher quality hazelnuts (GLMM: $Z = 7.33$, $p < 0.0001$).

Does the presence of others impact the eat-cache decision?

410 of the 2869 visits scored by observers for eat-cache decision outcomes at the feeder contained a competitive interaction ($n = 32$ squirrels, males = 17, females = 15). Within these 410 social visits each squirrel made on average 12.81 visits (min = 2 visits, max = 36 visits, SD = 8.91). 37% of the interactions occurred with a conspecific and 63% with a heterospecific (i.e., *O. beecheyi*). 75% of the observed interactions between gray squirrels ended in displacement of the squirrel at the feeder, 22% ended in both individuals staying at the feeder, and in 3% of cases the approaching squirrel left the feeder (Figure 3.3).

Squirrels were more likely to take an item from the feeder when no interaction occurred during their visit (GLMM: $Z = 6.88$, $p < 0.0001$) (Table 3.1c). However, the presence of a potential competitor during the visit did not predict the choice to eat or take an item, despite a

small non-significant trend towards a preference for eating (GLMM: $Z = -6.88$, $p = 0.49$). The outcome of the interaction (i.e., “displace,” “leave,” or “stay”) did influence the eat-cache choice, such that if a squirrel displaced another individual at the feeder, they were more likely to choose to take a cacheable item away from the feeder than to eat it (GLMM: $Z = 4.16$, $p < 0.0001$) (Table 3.1d). The species of squirrel involved in the interaction, or the sex of the individual had no impact on the decision.

Discussion

The goal of our study was to determine if squirrels adjust their eat-cache decisions in response to competition at an automated feeding station. Our results suggest that squirrels are monitoring the social environment and that they integrate this information into not only their decision to eat or cache, but into their decision to engage in foraging at the feeder in the first place. Our study brings to light two key insights: firstly, a greater proportion of feeder visits took place in solitary conditions, potentially underscoring avoidance of social interaction as a strategy of scatter hoarders as an initial line of defense against pilfering. Secondly, when interactions did occur at the feeder, squirrels adjusted their eat-cache decisions to strategically optimize their outcomes from the feeding station. Season, time of day, number of previous decisions already made, and food type were identified as predictors of the likelihood of social overlap occurring at the feeder. Further, squirrels were more likely to take a cacheable item from the feeder when foraging alone or when they were able to successfully displace any squirrels already at the feeder upon their arrival.

Overall, we recorded a higher frequency of solitary feeder visits during periods when this population has shown a preference for taking cacheable items from the feeding station (Robin et

al, *in prep*). We notice a concurrent decrease in the likelihood of social overlap during times of heightened prioritization of cacheable items, further underscoring the connection between caching behavior and interaction avoidance. This suggests a link between intensified caching and reduced tolerance for the presence of others. For instance, during the fall season when caching is most prominent, there is a decrease in tolerance for social overlap at the feeder in comparison to spring and summer. Similarly, there is an increased preference for caching during evenings and subsequently a lowered likelihood of social overlap in comparison to mornings and afternoons. Moreover, the preference for caching items like hazelnuts, which are highly storable, is further aligned with this trend of heightened caching and reduced tolerance for competitors.

Seasonal variations have predictable impacts on environmental food availability, exerting significant influences on food-storing behaviors as well as social behaviors like mating (Burger et al., 2013; Lavenex et al., 2000; Muul, 1969; Parker et al., 2014), which could in turn impact tolerance for social overlap at the feeding station. During spring and summer, squirrels were more likely to overlap at the feeding station compared to the fall. This aligns with previous findings from the same population, indicating that squirrels dedicated more time to eating rather than caching in the spring and summer months compared to fall (Robin et al, *in prep*). This pattern is consistent with the idea that during times of increased preference for storable food items, tolerance for social interaction is lower than during seasons in which there is an increased emphasis on immediate consumption of items while at the feeder. Further, increased eating at the feeder in spring and summer may extend visit durations, thereby fostering more opportunities for interaction. As caching behavior tends to become more routine in the fall, and in the presence of abundant food, squirrels might engage in rapid and extensive caching with reduced deliberation

and item valuation (Delgado et al., 2014). Consequently, fall visits to the feeder may be briefer overall, potentially limiting chances for social overlap.

The time of day influenced the occurrence of squirrels overlapping at the feeder. Specifically, squirrels exhibited a reduced likelihood of overlapping with others during evening visits to the feeder. This temporal pattern of decreased social overlap closely mirrors the observed seasonal trends, further reinforcing the connection between diminished tolerance for competition during times at which there is a heightened emphasis on collecting cacheable items from the feeder (Robin et al, *in prep*). This emphasizes the potential decrease in the acceptance of competition when focus is shifted from immediate consumption to storage. Additionally, visits to the feeder during the evening tended to be shorter on average compared to those in the morning or afternoon, potentially because the duration of a feeder visit was often lower when individuals take storable items instead of eating. As the selection of storable items peaks in the evenings, these expedited visits may consequently reduce the chances of social overlap. Further, the fewest number of visits to the feeder were recorded in the evening, with visits peaking in the morning and gradually tapering off as the day progressed (morning = 4901 visits, afternoon = 2350 visits, evening = 1470 visits). Consequently, the reduced frequency of visits during the evening will add to the decrease in potential for overlap between squirrels.

On a finer scale, the number of previous decisions made within a given day significantly influenced the probability of overlapping with other individuals at the feeder. As visits to the feeder increased, so did the likelihood of encountering another squirrel. However, while more opportunities for social overlap is an unavoidable cost to more visits to the feeder, they also were associated with a higher probability of selecting cacheable items – a choice that reduces visit duration and, consequently, the chance of social overlap. Instead, this trend may reflect a

diminishing concern for the presence of others as more food is stored. This is consistent with findings from other scatter-hoarding species in which increased amounts of stored food within foraging sessions leads to behavioral discounting in which there is a reduction in the perceived value of future items (Delgado et al., 2014). This may subsequently foster a higher tolerance for social competition. Further, it is also consistent with what would be expected if individuals were using a rapid sequestering approach, whereby they rapidly gather and store items, which could result in reduced concern for the presence of others due to their minimal investment in each cache (Delgado et al., 2014; Yi et al., 2019; Zhang et al., 2014).

The type of food available at the feeder played a crucial role in predicting the extent of overlap among individuals. Specifically, squirrels were more likely to tolerate increased competition at the feeder when peanuts (*Arachis hypogaea*) were present compared to hazelnuts (*Corylus avellana*). This pattern is reflective of the differential storabilities of the food items at the feeder. An item's storability is an index of traits that contribute to the duration of time a food item can remain viable if stored (Kotler et al., 1999). Food-hoarders must account for the storability of a food item when deciding to eat or cache (Juhasz et al., 2018; Sundaram et al., 2018; Xiao et al., 2013). The longevity of a seed's viability underground is influenced by its size and shell thickness, with larger seeds and those with thicker shells retaining viability for longer periods, unlike smaller, thinly shelled seeds (Lichti et al., 2017; Sundaram et al., 2015; Yi et al., 2021). Peanuts having thinner shells and being lower in calories have a lower storability than thicker shelled higher calorie hazelnuts (Delgado et al., 2014). Previous work has demonstrated a preference of *S. griseus* on this site for taking storable hazelnuts and opting to eat peanuts (Robin et al, *in prep*). Similar trends were observed in eastern fox squirrels who invested more time in caching hazelnuts than peanuts (Delgado et al., 2014). Thus, consistent with other predictors of

social overlap measured in this study, in contexts where storage is prioritized over eating, overlap at the feeder is less likely. By squirrels avoiding competition at times with more storable food is at the feeder individuals may decrease the risk those items will be pilfered.

Although solitary foraging was the dominant behavior recorded at the feeder, instances of interactions between both conspecific and heterospecific individuals were observed. These interactions were characterized by brief overlaps, signifying short encounters rather than prolonged engagements. Notably, *S. griseus* engaged more frequently with heterospecific individuals than conspecifics. However, interactions with heterospecifics were shorter in duration compared to interactions between gray squirrels. This suggests that interactions arising from interspecific competition could lead to unique responses, possibly influenced by varying perceptions of threat or competitive pressure. For instance, eastern gray squirrels have been observed to utilize evasive tactics like turning their backs or camouflaging empty cache sites when caching in the presence of conspecifics (Leaver et al., 2007). However, they do not deploy these measures when storing food in the presence of crows (Leaver et al., 2007). The competing squirrel species at our study site, *O. beecheyi*, are smaller in size and have been observed displaying submissive behaviors towards gray squirrels. Given this, *S. griseus* might demonstrate a greater tolerance for approaching the feeder when *O. beecheyi* is present compared to fellow gray squirrels. Upon the arrival of *S. griseus*, it's likely that *O. beecheyi* retreats, resulting in reduced overlap duration. This pattern aligns with the fact that a majority (75%) of social overlap instances at the feeder concluded with a displacement. Additionally, considering that California ground squirrels do not store food and as a result may be potentially less adept pilferers (Dittel et al., 2017; Vander Wall & Jenkins, 2003; Wang et al., 2018), they might not pose as significant a threat. Consequently, *S. griseus* can feed without disturbance due to the likelihood of the ground

squirrel fleeing upon their approach. Similarly, caching behavior might proceed uninterrupted, as California ground squirrels are potentially not as skilled at pilfering caches, further contributing to the reduced perceived threat during interactions.

Irrespective of the species, western gray squirrels exhibited modifications in their eat-cache decisions when encountering the presence of another squirrel. When foraging alone, squirrels displayed a heightened tendency to select to take storable items away from the feeder, potentially reflecting a strategy to mitigate pilfering risks by prioritizing storage during periods of reduced social competition. This further aligns with the rapid sequestering hypothesis, where squirrels aim to deplete as many resources as possible from a patch before the foraging site becomes apparent to others (Zhang et al., 2014). Additionally, squirrels engaged in interactions at the feeder that ended in displacing the other individual, were more likely to take a cacheable item from the feeder than to eat. This reflects the tendency of the focal squirrel to prioritize storage after eliminating direct social competition in the vicinity and is consistent with our broader findings that suggest a heightened likelihood of prioritizing taking cacheable items while foraging alone. Moreover, the heightened awareness of competition post-interaction might prompt squirrels to rapidly cache items from the site, capitalizing on the opportunity to exploit patch resources before competitors return.

This study's findings shed light on the interplay between the social environment and eat-cache strategies in western gray squirrels, underscoring their adaptability in the face of competition. Solitary foraging prevailed as a dominant strategy while visiting the feeder, potentially as a defense mechanism against theft, especially during seasons and times when caching is typically prioritized. Further, interactions prompted strategic adjustments in eat-cache decisions, such that squirrels favored taking cacheable items from the feeder when foraging alone

or after displacing others. It is important to acknowledge two potential limitations to these findings. First, the presence of another squirrel during the eat-cache decisions recorded here was defined by overlap at the feeder, meaning both squirrels were scanned by the PIT-tag antenna at once. This requires individuals to be in close proximity to one another. It is likely that there were other squirrels in the general vicinity of the feeder that were not recorded as social overlap but could have influenced the decisions made at the feeder. Further, this method excludes squirrels visiting the feeder that are not PIT-tagged. Second, we do not have data on confirmed caches, instead we assume the prioritization of storage when a cacheable food item is selected and removed from the feeder and not seen or heard being eaten on the surrounding cameras. The absence of confirmed caches raises the possibility that squirrels' remove items from the feeder to consume elsewhere due to social competition or predation risk. However, most items eaten while at the feeder were the in-shell cacheable food items over the immediately available minced nuts. Thus, we do find it reasonable to assume many in-shell items removed from the feeder were intended for storage over consumption.

Overall, our findings underscore the squirrels' responsiveness to the social environment not only in their eat-cache choices but also in their decision to engage in foraging activities. Scatter-hoarding is a cognitive-intensive strategy, requiring individuals to navigate multiple challenges at several levels while simultaneously accounting for environmental and state-dependent factors (Delgado et al., 2014; Delgado & Jacobs, 2017; Greenberg & Zarnoch, 2018; Leaver et al., 2007; Robin & Jacobs, 2022; Samson & Manser, 2016a; Steele et al., 2008, 2015; Sutton et al., 2016; Vander Wall, 2000). The social environment is no exception; the decision to forage, to eat or cache found items, selection of storage sites, caching procedures, memory, and retrieval strategies are all in part molded by competition. This behavioral adaptability not only

sheds light on the cognitive intricacies of scatter-hoarding but also underscores the broader principle that seemingly solitary species are influenced by their social environment. Looking ahead, exploring additional dimensions such as competition from food-storing birds and individual personalities promises to deepen our understanding of how social factors shape wildlife behavior

Table 3.1: Parameter estimates of the highest performing GLMMs for each model set.

	FIXED EFFECT	ESTIMATE	STD. ERROR	Z VALUE	PR(> Z)	ODDS RATIO	95% CI	
(a.)	THE SPECIES A SQUIRREL OVERLAPS WITH AT THE FEEDER IS PREDICTIVE OF THE DURATION OF THE VISIT.	Overlap – Gray squirrel (Intercept)	0.55954	0.02438	22.947	<2e-16	0.94	0.89-0.99
		Overlap – Ground Squirrel	-0.06312	0.02622	-2.407	0.0161		
(b.)	SEASON, NUMBER OF PREVIOUS VISITS, TIME OF DAY, AND FOOD TYPE IS PREDICTIVE OF WHETHER SOCIAL OVERLAP WILL OCCUR.	Season – Fall Afternoon (Intercept)	-1.80524	0.128233	-14.0778	<2e-16	0.16	0.36-0.62
		Season – Spring	0.577766	0.097862	5.903911	3.55E-09	1.78	-2.06–1.55
		Season – Summer	0.688358	0.091009	7.563588	3.92E-14	2.00	0.39-0.77
		Number of previous visits	0.00423	0.002045	2.06802	0.0386	1.00	0.51-0.87
		Time of Day – Evening	-0.63361	0.098091	-6.45935	1.05E-10	0.53	0.00-0.01
		Time of Day – Morning	0.053034	0.067677	0.783639	0.4333	1.05	-0.83–0.44
(c.)	THE PRESENCE OF SOCIAL OVERLAP AT THE FEEDER IS PREDICTIVE OF A SQUIRREL’S EAT-CACHE DECISION.	Social – No Overlap	1.02894	0.14956	6.88	6.00E-12	2.80	0.60-1.09
		Social – Yes Overlap	-0.08718	0.1267	-0.688	0.491	0.92	0.73-1.34
(d.)	THE OUTCOME OF THE SOCIAL INTERACTION IMPACTS THE EAT-CACHE DECISION.	Social Outcome – Displace	0.9236	0.222	4.16	3.19E-05	0.73	0.64-0.80
		Social Outcome – Leave	0.3194	7.307	0.437	0.662	0.76	0.46-0.94
		Social Outcome – Stay	0.3396	0.976	1.141	0.254	0.79	0.67-0.87
		Species Overlap – Gray Squirrel	0.1544	0.2605	0.593	0.553	0.76	0.66-.0.84

Figure 3.1: Proportion of visits with and without social interactions. 8,610 total visits collected from 39 western gray squirrels. 77% of all visits did not contain any social interactions, in 5.8% of visits individuals interacted with another western gray squirrel, and 17.5% of visits squirrels interacted with a California ground squirrel.

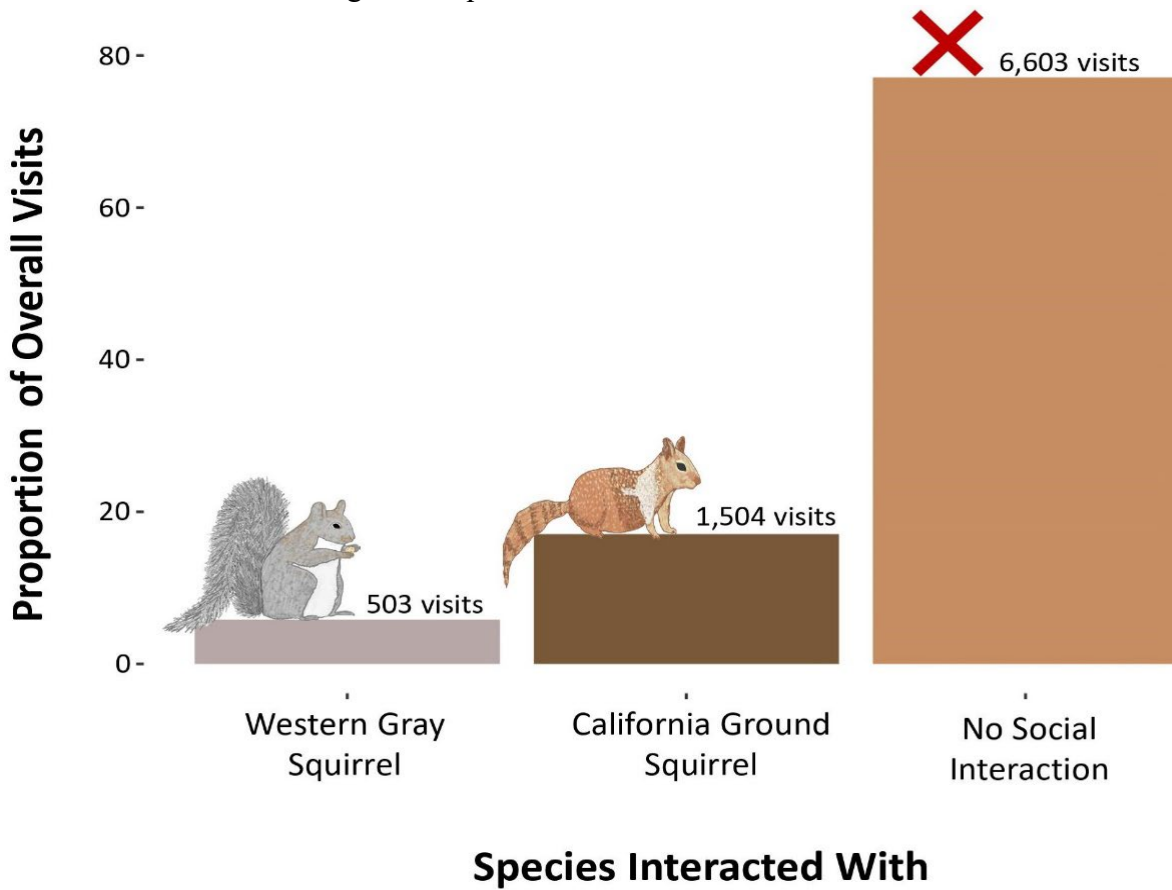


Figure 3.2: Proportion of visits with social interactions by season, time of day, and food type. Squirrels are more likely to forage at the feeder alone. However, the occurrence of social overlap was predicted by season, time of day, and food type. Season predicted the occurrence of overlap at the feeder such that squirrels were more likely to overlap in the summer and spring than in fall. Interactions between individuals were also more likely in the morning and afternoon than in the evening and when peanuts were available in comparison to when hazelnuts were available.

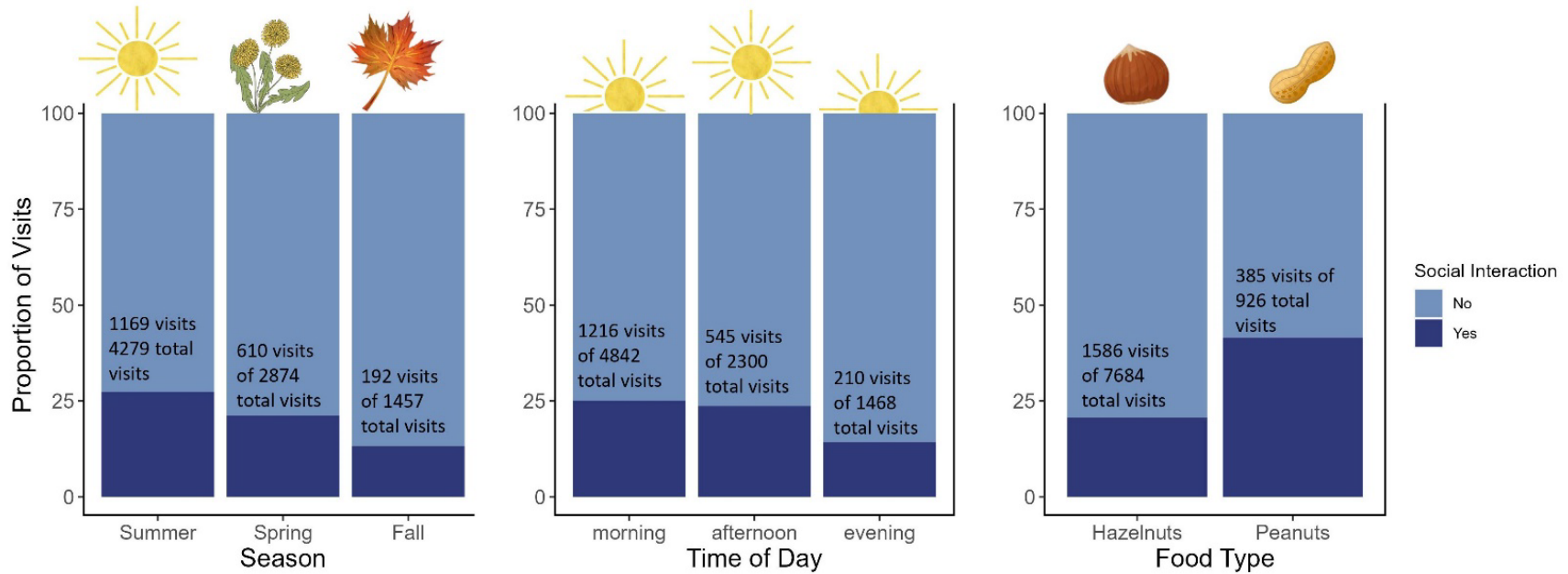
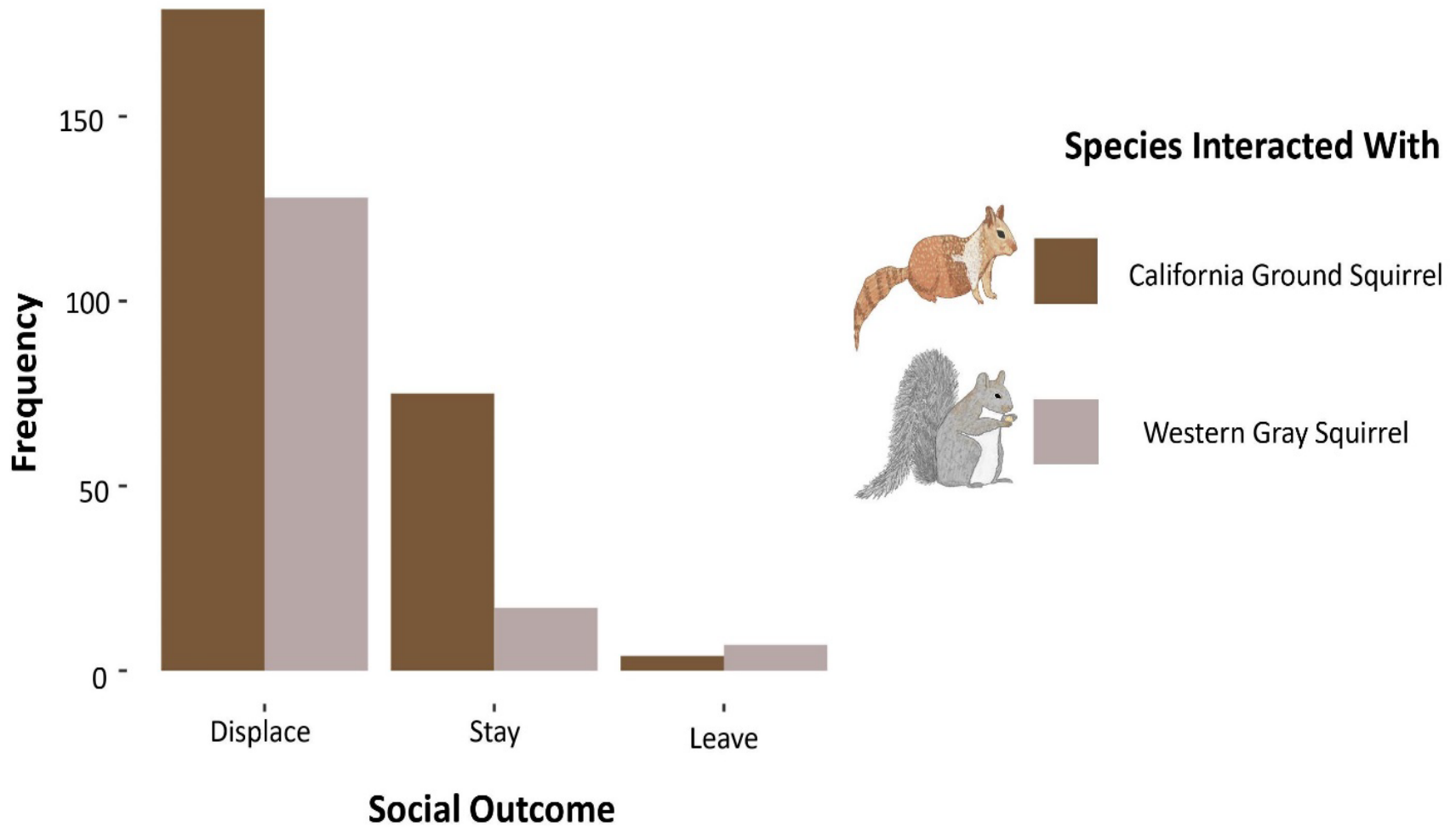


Figure 3.3: Counts of outcomes of social interactions by species. Out of the 2,869 total visits scored for social interaction at the feeder, 410 contained a social interaction. 75% ended in the squirrel already at the feeder being displaced (California ground squirrel = 179, western gray squirrel = 128). In 22% of cases both squirrels remained at the feeder (California ground squirrel = 75, western gray squirrel = 17), and in 3% of cases the squirrel showing up at the feeder left upon arriving and seeing another squirrel already at the feeder (California ground squirrel = 4, western gray squirrel = 7).



Appendix S3.2: Selected variables and Akaike's information criteria (AIC) values of top ten ranked models for each model set. '+' indicates variable was included in model. Rank '*' best performing interaction model, outperforms highest ranked model.

	RANK	AGE	SEASON	SEX	TEST	TIME OF DAY	NUMBER OF PREV.DECISIONS	OVERLAP SPECIES	LOGLIK	AIC	Δ AIC
(a.) THE SPECIES A SQUIRREL OVERLAPS WITH AT THE FEEDER IS PREDICTIVE OF THE DURATION OF THE VISIT.	1*							+	-2278.0	4563.906	0
	2				+				-2279.7	4567.478	3.572931
	3		+					+	-2277.8	4567.692	0.214018
	4	+			+				-2279.2	4568.476	0.783949
	5	+							-2280.5	4568.977	0.500306
	6		+				+		-2277.6	4569.209	0.232364
	7				+				-2280.8	4569.692	0.483059
	8						+		-2280.8	4569.699	0.006678
	9			+	+		+	+	-2277.6	4571.102	1.403255
	10	+	+	+	+	+	+	+	-2273.6	4571.186	0.083483
(b.) SEASON, NUMBER OF PREVIOUS VISITS, TIME OF DAY, AND FOOD TYPE IS PREDICTIVE OF WHETHER SOCIAL OVERLAP WILL OCCUR.	1*		+		+	+	+	NA	-4365.78	8747.556	0
	2		+	+	+	+	+	NA	-4365.76	8749.52	1.964425
	3			+		+	+	NA	-4365.76	8749.524	1.967948
	4			+		+		NA	-4367.86	8749.719	2.163529
	5	+	+	+	+	+	+	NA	-4365.75	8751.5	3.944145
	6		+	+	+	+		NA	-4367.84	8751.681	4.124944
	7	+	+		+	+		NA	-4367.85	8751.69	4.134525
	8	+	+	+	+	+		NA	-4367.83	8753.663	6.107564
	9			+		+	+	NA	-4392.07	8798.133	50.57751
	10	+	+			+	+	NA	-4392.03	8800.063	52.50709

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